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SELECTION RESPONSE IN A MULTI-BREED SYNTHETIC BEEF CATTLE POPULATION COMPARED TO THAT FROM A PUREBRED HERD

by

© LINDEN WILLMS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SELECTION RESPONSE IN A MULTI-BREED SYNTHETIC BEEF CATTLE POPULATION COMPARED TO THAT FROM A PUREBRED HERD submitted by LINDEN WILLMS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE in ANIMAL BREEDING.

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Date May 8, 1981

ABSTRACT

The response to selection in a purebred Hereford population and a multi-breed Synthetic population was compared. Birth weight, weaning weight and preweaning average daily gain (ADG) were examined in both sexes. Postweaning ADG and 365-day weight were examined in males while 18-month weight was examined in females. Heritability and selection intensity values were estimated in both populations and applied in calculating expected genetic responses. Annual expected genetic responses for birth weight, preweaning ADG and weaning weight in the Hereford population were: 0.11 kg, 2.65 g/day and 0.69 kg. The respective values for the Synthetic population were: 0.38 kg, 9.30 g/day and 1.80 kg. Genetic gains expected in postweaning ADG and 365-day weight in males were 18.3 g/day and 5.1 kg per year for the Hereford population. Those for the Synthetic population were 23.4 g/day and 6.2 kg.

Realized genetic response was estimated using 3 methods, a control population, Best Linear Unbiased Prediction analysis and repeat matings. Problems were encountered with all methods, however the repeat matings method yielded the best results for preweaning traits. Annual genetic gains in birth weight, preweaning ADG and weaning weight for the Hereford population were -0.26 ± 0.12 kg, 3.25 ± 2.72 g/day and 0.13 ± 0.60 kg while those for the Synthetic population were -0.27 ± 0.10 kg, 7.76 ± 3.25 g/day and 0.93 ± 0.53 kg. No reliable estimates were calculated

for postweaning traits. However, the results indicated a greater positive genetic gain for all postweaning traits in the Synthetic population than the Hereford population. The conclusion drawn was that the genetic response to selection was greater in the more heterozygous Synthetic population than in the purebred Hereford population.

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I. Introduction

Selection is a force, partially controlled by the breeder, directed at changing phenotypic traits in a particular population. Through selection, genes and gene combinations which code for favorable phenotypes are thought to be maintained at a high level. Most selection in beef cattle has been applied in individual herds within breeds with almost none being reported in crossbred or multi-breed populations. The aim of this research is to examine the effects of selection on a multi-breed population, or a Synthetic breed of beef cattle and compare these effects with those of a more traditional purebred Hereford population treated in similar fashion. Practically, this leads to a critical analysis of the traditional approach of selection within breeds with subsequent crossing of the breeds. Since purebred beef cattle are generally less productive than their related crossbreds, one may question whether purebreds are necessary.

If the desireable phenotypic characters of several purebred breeds were incorporated into a crossbred population and selection practiced in this population, perhaps genetic responses would equal or exceed those experienced in purebred populations. Genes and gene combinations which would normally not exist in any one breed would be expressed in a multi-breed population. These genes and gene combinations would be tested under selection, and those that result in the superior phenotype would be

retained.

The genetic heterogeneity of the population would result not only in the maintenance of hybrid vigor, but also in providing for a greater degree of adaptability to changes in environment. Responses to selection would be expected to be greater in a crossbred population than in a more genetically homozygous purebred one.

The traits examined were birth weight, preweaning average daily gain and weaning weight, sex ignored; postweaning average daily gain and yearling weight in males, and 18-month weight in females.

Phenotypic time trends may be of environmental or genetic origin. Since the genetic changes are of particular interest in a breeding program, they must be separated from the environmental. Various methods have been developed to isolate genetic trends. Of these, three are applicable to the data in the present study and will be applied. These methods include: (1) comparison of selected populations with a control population, (2) use of repeat matings to estimate environmental trends and (3) the estimation of the rate of change of sire breeding values as predicted by Best Linear Unbiased Prediction (BLUP) procedures.

II. Literature Review

Since their domestication , man has attempted to improve the performance of animals and breed types which conform to his ideals. Thus, distinctive breeds came into being, each influenced by the environment in which it was developed, the functional capabilities demanded of it, and the cultural and aesthetic whims of the breeder. Most of the present breed differences are as a result of natural or artificial selection driven by these forces.

As greater importance was placed on performance traits such as reproductive ability, growth potential and carcass quality, selection within breeds occurred and systems of breeding and selection were developed in an attempt to improve these traits.

During the past century, most breeding programs in beef cattle have centred around inbreeding. Attempts were made to fix the genes of a superior individual into the population. By linebreeding or inbreeding with selection, it was felt that these favourable genes would become homozygous and replace many of the less favourable recessive genes normally masked in the heterozyous state. Some of the present-day breeds of beef cattle were developed in this manner (Lasely 1963).

Relatively few studies report the genetic response to selection under inbreeding. Flower *et al.* (1964) reported estimates of positive genetic trends for birth weight and weaning weight in closed lines of Hereford cattle. Brinks *et*

al. (1965) studying the Line I Hereford cattle at the U.S. Range Livestock Experimental Station at Miles City, Montana, reports a detrimental effect of inbreeding on both preweaning and postweaning traits. After adjusting for inbreeding effects, the genetic response to selection estimated for birth weight, preweaning gain, weaning weight and weaning score was positive. Other, more recent work, has confirmed these results; genetic gains due to selection are possible but inbreeding normally has a negative effect, with traits controlled by non-additive gene action being affected the most (Bailey *et al*. 1971; Chevraux *et al*. 1977).

Studies with field crops, especially corn, demonstrated a dramatic increase in vigor and productivity when two inbred lines were crossed. This increase afforded some justification in developing low producing inbred lines which in turn could be crossed. It was felt that selection within the lines would result in homozygosity for favourable genes and crossing would contribute to non-additive effects with a possible heterotic effect.

This same principle has been carried over to beef cattle breeding where crossbreeding involving 2 or more distinct breeds has increased in importance over the past 20 years. Multiple plans for crossing are available (Warwick and Legates 1979). All attempts were to maximize both heterosis and the frequency of desirable genes with additive effects. To maximize heterosis, breeds with diverse genetic backgrounds are combined; to ensure the maximum frequency of

desirable genes, selection for these genes within the foundation breeds is assumed. Most crossbreeding plans demand that the *F1* or *F2* crossbreds be marketed and new breeding stock be regularly introduced from purebred stock. In this way, there is seldom selection for production carried on within the crossbred population.

Limited research has been conducted on selection within a crossbred population, which if carried out may lead to the development of a new breed. Most recent cases of this occurring are the development of breeds such as the Beefmaster (Lasater 1968) and Santa Gertrudis (Rhoad 1949) which are crosses between *Bos taurus* and *Bos indicus* species. The Norwegian Red breed embraces all other existing breeds in Norway with selection occurring across all foundation breeds, resulting in the development of a new breed (Syrstad 1967).

Dickerson (1969) theorizes three possible shortcomings in the process of formation of new breeds as an alternative to breeding schemes for systematic use of hybrid vigor: (1) lower level of heterozygosity maintained; (2) loss of the maternal component of heterosis; (3) loss of favorable epistatic combinations fixed in the parental breeds. The factors to be considered in evaluating a selection program in a synthetic population are the number of generations needed for a synthetic to recover from the loss of heterosis (if this occurs) after the initial crosses and the number of generations needed for the synthetic to surpass the level of

performance of its best parent (Lopez-Fanjul 1974). Where synthetic breeds have been formed, the evidence that they eventually surpass the performance of their better parental stock or their F1 is lacking. A loss of heterosis from the F1 to the F2 has been reported in weight from weaning to 18 months in Brahman X Devon crosses (Kidder *et al.* 1964). Cartwright *et al.* (1964) report similar results for body weight and daily gain in Brahman X Hereford crosses under semi-intensive conditions. On the other hand, the Brahman X Hereford F2 crosses showed a considerable maternal component of heterosis, reflected in a superiority of the F2 over the F1 for 6-month body weight and calving and weaning percentages.

Dickerson (1969) suggests that a synthetic population may show an increase in variability compared to the average of its constituent populations and thus provide larger selection gains for future generations. However, this has not been demonstrated. Australian data on birth weight in Hereford and Shorthorn cattle and their F1 and F2 crosses revealed very little extra variation in the F2 (Seifert and Kennedy 1966). Robertson (1949) in reviewing earlier literature concluded that the extra variation in the F2 crosses between European and tropical breeds was negligible for milk and milk components.

III. Data

A. Breeds

Data for this study consist of records collected from 1962 to 1978 on two herds of beef cattle owned by The University of Alberta. The herds were composed of a purebred Hereford population and a synthetic population which has been developed by the University. A description of the breeding populations follows.

Hereford

The original females which made up the Hereford population were purchased from four Alberta breeders in 1960. Together with those females already owned by the University, the foundation herd of 79 females was established (Berg 1962). The male foundation was made up of two Hereford bulls owned by the University and three Hereford bulls loaned from Alberta breeders (Berg 1964). Although the Hereford population has been basically closed, a small number of outside sires, selected on the basis of superior performance or progeny tests have been introduced by artificial insemination (A.I.) each year. Progeny from these sires were allowed to compete, on merit of their own performance, for a place in the breeding program of the Hereford population (Berg 1971).

Beef Synthetics

The Beef Synthetic population,which will hereafter be referred to as the Synthetic population, originated in 1960

with the purchase of Angus, Angus x Charolais and Galloway females from five Alberta breeders (Berg 1962). These animals, together with a few Angus heifers already owned by the University formed the female foundation stock. Three Galloway and two Angus bulls were initially used in the herd (Berg 1964). In the eight years subsequent to this, a wide sampling of Charolais sires were mated by A.I. to the predominantly Angus and Galloway females. This formed the basis for the herd and very little outside genetic material has since been introduced (Berg 1975). Small amounts of Brown Swiss, Hereford, Holstein, Jersey and Brahman were introduced through impure foundation animals.

The breeds which are combined in the Synthetic population were intended to complement each other in their strong characteristics. Charolais were included for growth and muscling, Angus for carcass quality, and Galloways for winter hardiness (Berg 1975). Under selection, it was assumed that as the most desirable phenotype developed the relative genetic contribution of each breed would arrive at an equilibrium. The average breed percentages in the Synthetic calves born from 1962-1977 are shown in Table 3.1.

Table 3.1. Breed Composition of the Synthetic Population'

BREED	1962	1966	1970	1974	1978
Angus	41.1	41.6	37.6	36.0	35.7
Charolais	16.8	29.8	35.1	34.4	34.7
Galloway	40.3	26.4	20.3	21.4	21.7
Brown Swiss	0.0	0.6	4.7	4.2	4.5
Others	1.5	1.6	2.3	4.0	3.4

'Values within a column give the percentage of the total.

B. Management

Management practices of the breeding populations have been described in detail by Berg (1978). Mature females of all breeds were ranged together year round except for a 2 month breeding period in July and August when they were separated into single sire breeding groups. Supplemental feeding of straw, hay and grain were supplied to provide for the basic maintenance requirements for cows and heifers in the winter. First-calf heifers were fed to gain a moderate amount of weight (10-20 kg) prior to calving while mature females were fed to maintain their precalving weight.

Yearling and 2-year-old heifers were separated from older cows during the winter. Heifers, which had been bred to calve as 2-year-olds, were calved separately in a semi-enclosed feedlot area, while mature cows calved on the open range. The first-calf heifers remained separated until the following breeding season.

Calves were weighed at birth and monthly to weaning at approximately 5 months of age. No creep feed was provided during the preweaning stage. All bull calves were left

intact and since 1966 had been fed a high concentrate ration *ad libitum* during a 140-day feeding trial. Heifers were fed the first winter to gain approximately 0.5 kg per day.

C. Selection Practices

Selection practices have been outlined by Berg (1975). The major criterion for bull selection was weight for age at approximately one year of age. Some negative selection was placed on extremely heavy birth weights and all bulls delivered by surgery were not eligible to be selected for breeding. Type played no role as a criterion in selection. Most bulls were used as yearlings with approximately 25% being repeated for a subsequent year.

Up to 1966 heifer replacements were selected on the basis of weight for age at 18 months of age. However, since 1967, all sound heifers have been exposed to bulls and those that failed to conceive were culled.

Culling of cows was predominantly on reproduction with some culling occurring on calf weaning weights, and unsoundness or defects such as requiring caesarian section, eversion of the reproductive tract, bad udders, or disease. All females 2 years of age and older, failing to produce a calf each year were culled. In the Synthetic population, some selection of 5-year-old dams on their progeny performance occurred. This was not possible in the Hereford population where all producing cows had to be kept to maintain population size.

IV. Adjusting the Data

A. Introduction

Selection and genetic improvement in a breeding program is based on the accuracy of identifying genetically superior animals. Environmental factors affect the growth of individuals and as such may obscure true genetic differences. Some of these environmental effects may be minimized by treating all animals alike, while others may be controlled statistically. Age and sex of calf and age of dam are three factors which can be adjusted statistically, bringing all data to a common base, i.e., calf of a common age and sex and from a common age of dam.

For postweaning traits, analyses are generally computed within sex; however, for preweaning traits analyses across sexes are often necessary. This is especially true where sires are being evaluated on their progeny's performance or where genetic trends of preweaning traits are being estimated.

The effects of sex of calf and age of dam on preweaning and postweaning traits are well documented for the Hereford breed (Cundiff *et al* 1966; Schaeffer and Wilton 1974; Pabst *et al* 1977; Anderson and Wilham 1978). However, very little information exists on the effects of these factors in multi-breed or synthetic populations of beef cattle. Also, in studies reporting multiplicative and additive adjustment factors for sex of calf and age of dam, the method of

applying these factors to the data is rarely given.

The purpose of this study was to estimate the effects of sex of calf and age of dam on birth weight, preweaning ADG and weaning weight. The effect of age of dam will be estimated for postweaning ADG and yearling weight in males and 18-month weight in females. Comparisons of these effects will be made between the 2 populations of cattle. Adjustment factors will be derived and the appropriate method of applying these factors to the data will be determined.

B. Material and Methods

All animals from 1962-1978 with complete preweaning data were included in the analyses of preweaning traits. Animals with missing birth weights or weaning weights were deleted. Cases which involved twins, foster dams or any other abnormal mothering conditions were also dropped.

The data were edited further for the analysis of postweaning traits. Analysis of yearling weight and postweaning ADG was performed for males only. Since the feed test ration for males changed drastically in 1966, all data previous to that date were omitted from the analysis. Only those males with a final yearling weight recorded were included. In addition, all animals receiving rations different from the standard test ration were deleted. This deletion included animals tested at the Provincial Record of Performance(ROP) center or involved in special research projects. All females from 1962-1977 with 18-month weight

records were included in the analysis of 18-month weight. Frequency of observations by breed and traits are shown in Table 4.1.

Adjustment for Age of Calf

Since not all calves were born on the same day and weighings were often not practical on exact end point dates, adjustments to the data for age of calf were necessary.

Weaning occurred in October when calves ranged from 120 to 190 days of age. Previous studies have shown that a linear relationship exists between age at weaning and preweaning ADG for 120 to 250 days of age (Schaeffer and Wilton 1974). This relationship was assumed for the present study and adjusted 180-day weaning weights were calculated by:

Adj.weaning weight=180*(preweaning ADG)+birth weight

where,

$$\text{Preweaning ADG} = \frac{\text{actual weaning weight-birth weight}}{\text{age at weaning}}$$

Yearling weight for bulls was calculated by adjusting the final weight of the 140-day feed test period to a 365-day of age basis using the following formula:

Table 4.1. Distribution of observations by breed and trait.

Breed	Trait		
	Preweaning[1]	Postweaning Males[2]	Postweaning Females[3]
Hereford	1091	371	459
Synthetics	1714	623	746
Totals	2805	994	1205

[1]Includes 1962-1978
[2]Includes 1966-1978
[3]Includes 1962-1977

Table 4.2. Distribution of observations of preweaning data by age of dam and sex within breed.

Age of Dam (yr)	Hereford		Synthetic	
	Males	Females	Males	Females
2	118	121	190	192
3	102	97	179	165
4	85	88	153	144
5	85	60	132	104
6+	168	167	214	241
Totals	558	533	868	846

Adj.yearling weight = adj.180-day weight + 185*(Test ADG)

where,

$$\text{Test ADG} = \frac{\text{final weight on test-initial weight on test}}{\text{no. of days on test}}$$

All heifers were weighed at approximately 18 months of age from which an adjusted 18-month weight was calculated in the following manner:

$$\text{Adj. 18-month weight} = \text{adj.weaning weight} + \frac{360 * (\text{actual 18-month weight-actual weaning weight})}{(\text{18-month weighing date-weaning date})}$$

Adjustment for Sex of Calf and Age of Dam

Preweaning traits

All heifers entering the breeding populations calved for the first time at 2 years of age. Other workers have found no significant effect of age of dam on preweaning traits after 5 years of age (Cardellino and Frahm 1974; Schaeffer and Wilton 1974). However, in the present study, preliminary analysis demonstrated an additional effect between 5- and 6-year-old dams. Thus, dams were grouped into 2-, 3-, 4-, 5- and 6+-year-old groupings based on year of

birth of the dam. Distribution of observations by age of dam and sex within breed are shown in Table 4.2.

Data for birth weight, preweaning ADG and weaning weight were analysed within breed using the least-squares procedure according to Harvey (1970). The following model was assumed for the analyses:

$X_{ijklm} = U + B_i + S_j + A_k + Y_l + BS_{ij} + BA_{ik} + SA_{jk} + BSA_{ijk} + BY_{il} + SY_{jl} + E_{ijklm}$

where

X_{ijklm} = an observed preweaning growth trait.

U = the population mean.

B_i = the effect common to calves of the ith breed.

S_j = the effect common to calves of the jth sex.

A_k = the effect common to calves from the kth age of dam.

Y_l = the effect common to calves born in the lth year.

BS_{ij} = the effect common to calves of the ith breed and the jth sex.

BA_{ik}= the effect common to calves of the ith breed and from the kth age of dam.

SA_{jk} = the effect common to calves of the jth sex and from the kth age of dam.

BSA_{ijk} = the effect common to calves of the ith breed and the jth sex from the kth age of dam.

BY_{il} = the effect common to calves of the ith breed born in the lth year.

SY*jl* = the effect common to calves of the *j*th sex born in the *l*th year.

E*ijklm* = the random error associated with a preweaning growth record on the *m*th calf.

In addition, preweaning ADG and adjusted weaning weight were analysed with birth weight as a covariate in the model.

Postweaning traits

Preliminary analyses of postweaning traits indicated no age of dam effects in dams greater than 4 years of age. Thus, only three age of dam subgroups (2-, 3- and 4+-year-olds) were included in the analyses of these traits in both males and females. Table 4.3 gives the distribution of observations within breed and age of dam.

Analyses for all postweaning traits were carried out within breed and sex according to the following model:

$$X_{ijklm} = U + B_i + A_k + Y_l + BA_{ik} + BY_{il} + E_{ijklm}$$

where

X*ijklm* = an observed postweaning growth trait.

U = the population mean.

B*i* = the effect common to animals of the *i*th breed.

A*k* = the effect common to the animals from the *k*th age of dam.

Y*l* = the effect common to animals born in the *l*th year.

Table 4.3. Distribution of observations of postweaning data by age of dam and sex within breed.

Age of Dam (yr)	Hereford		Synthetic	
	Male[1]	Female[2]	Male[1]	Female[2]
2	111	108	169	173
3	87	77	150	148
4+	290	274	448	425
Totals	488	459	767	746

[1]Includes data from 1966-1978
[2]Includes data from 1962-1977

BA*ik* = the effect common to animals of the *i*th breed and the *k*th age of dam.

BY*il* = the effect common to the animals of the *i*th breed born in the *l*th year.

E*ijklm* = the random error associated with a postweaning growth record of the *m*th animal.

C. Results and Discussion

Main Effects and Interactions

Preweaning traits

Analyses of variance indicated highly significant ($P<.01$) effects for all main factors--breed, sex of calf, age of dam and year, for all three traits--birth weight, preweaning ADG and weaning weight (Table 4.4). Only the effects of breed, sex of calf and age of dam together with all 2-way and the 3-way interactions involving these effects are discussed in this study.

Overall, Synthetics weighed 2.03 kg heavier than the Herefords at birth (Table 4.5). The non-significant ($P>.05$) breed x age of dam and sex of calf x age of dam interactions for birth weight suggest that the effect of age of dam was the same in both breeds and sexes. In view of the fact that interactions do occur in subsequent growth phases of the calf, the lack of these interactions in birth weight may reflect the protective influence of the intrauterine environment.

The Synthetics gained 163.0 g/day more than the Herefords and weighed 31.4 kg more at weaning (Table 4.6). Hereford males gained 35.0 g/day more than Hereford females and Synthetic males gained 69.0 g/day more than Synthetic females. The corresponding values for weaning weight are 8.3 kg and 14.6 kg. The breed x sex interaction was found to be highly significant ($P<.01$). This interaction is probably partly due to the

Table 4.4. Analyses of variance for birth weight, preweaning ADG and weaning weight.

Source	df	Mean Squares		
		Birth Weigh (kg)	Preweaning ADG (kg/day)	Weaning Weight (kg)
Breed (B)	1	5274.63**	33.863**	1253690.51**
Sex (S)	1	6607.96**	3.321**	167769.59**
BS	1	84.53	.342**	13034.30**
Age of Dam (A)	4	6188.49**	4.469**	210550.37**
BA	4	11.70	.077*	2346.53
SA	4	71.10	.072*	2639.25*
BSA	4	38.59	.059	2428.20
Years (Y)	16	713.39**	1.206**	45843.48**
BY	16	88.79**	.099**	3430.13**
SY	16	80.15**	.033	1237.50
Residual	2737	36.99	.029	1056.51

* P<.05
** P<.01

superior milking capacity of the Synthetic cows over the Hereford cows. In a previous report (Butson *et al.* 1977), using data from the same herds as in the present study, it was found that milk yield in the Synthetics was about 17% higher than the Herefords, measured by

Table 4.5. Least squares means and standard errors for birth weight (kg) by breed and sex.

Age of Dam (yr)	Hereford		Synthetic	
	Male	Female	Male	Female
2	30.82 ± .39	28.67 ± .39	32.55 ± .30	30.97 ± .30
3	32.82 ± .41	31.19 ± .43	35.48 ± .31	32.72 ± .32
4	34.79 ± .44	32.30 ± .44	37.10 ± .33	34.09 ± .34
5	36.02 ± .45	33.53 ± .53	38.61 ± .36	35.23 ± .41
6+	36.35 ± .32	34.74 ± .32	38.22 ± .28	36.31 ± .26
Ages of Dams Pooled	34.11 ± .18	32.09 ± .19	36.39 ± .14	33.87 ± .15
Sexes Pooled	33.10 ± .11		35.13 ± .13	

milkings in June and September. Male calves may have a greater nutritional requirement than female calves and as such, Hereford males were not able to express their full growth potential. Other workers have found no breed x sex interaction (Schaeffer and Wilton 1974; Cardellino and Frahm 1974). However, they were comparing Angus and Hereford breeds which do not differ greatly in milk production.

Combined with the increased milk production in the Synthetics, additive gene effects contributed by the Charolais breed, as well as the heterotic effects of a

Table 4.6. Least square means and standard errors of Hereford and Synthetic preweaning ADG and weaning weights.

	Preweaning ADG (g/day)			
	Hereford		Synthetic	
Age of Dam (yr)	Male	Female	Male	Female
2	720 ± 11	658 ± 10	859 ± 8	807 ± 8
3	737 ± 11	744 ± 12	940 ± 8	882 ± 9
4	819 ± 12	765 ± 12	999 ± 9	914 ± 9
5	841 ± 12	799 ± 14	1005 ± 10	935 ± 11
6+	837 ± 9	807 ± 9	1041 ± 8	970 ± 7
Ages of Dam Pooled	790 ± 5	755 ± 5	969 ± 4	900 ± 4
Sexes Pooled	772 ± 5		935 ± 3	
	Weaning Weight (kg)			
	Hereford		Synthetic	
2	160.3 ± 2.1	147.0 ± 2.0	187.0 ± 1.6	176.2 ± 1.6
3	165.1 ± 2.1	165.1 ± 2.3	204.5 ± 1.6	191.5 ± 1.7
4	182.2 ± 2.4	169.9 ± 2.3	216.8 ± 1.7	198.5 ± 1.8
5	186.5 ± 2.4	177.3 ± 2.8	219.4 ± 1.9	203.4 ± 2.1
6+	186.8 ± 1.9	180.0 ± 1.7	225.6 ± 1.5	210.8 ± 1.4
Ages of Dam Pooled	176.2 ± 1.0	167.9 ± 1.0	210.7 ± 0.9	196.1 ±
Sexes Pooled	172.0 ± .7		203.4 ± .6	

more heterozygous genotype, resulted in a greater response in growth in the Synthetic population. The same effect was apparent in the significant ($P<.05$) age of dam x sex of calf interaction. The 2-year-old dams were better able to fulfill the nutritional requirements of their calves than were 3-year-old dams. The requirements of suckling a calf as well as supporting continued body growth imposed a stress on the 2-year-old dam which affected her performance as a 3-year-old. As a result, calves from 3-year-old dams were most likely to experience nutritional stress.

The sex of calf x age of dam interaction for both preweaning ADG and weaning weight were largely due to the poor performance of Hereford male calves from 3-year-old dams. Least squares means for preweaning ADG and weaning weights did not differ between Hereford male and female calves from these dams. This result again reflects the inability of the Hereford dam to fulfill the nutritional requirements of the male calves.

The breed x age of dam effect was significant ($P<.05$) for preweaning ADG but not significant ($P>.05$) for weaning weight. The difference in significance, however, was very slight and is not considered important. In the Herefords, very little increase was evident in preweaning ADG and weaning weight in calves from dams over 5 years old. This finding agrees well

with the literature where the effects of age of dam on preweaning growth are relatively small in dams older than 5-year-olds (Schaeffer and Wilton 1974). On the other hand, there was still a significant increase in these traits when considering the difference between calves from 5- and 6+-year-old dams in the Synthetics. This result may reflect the later maturation of the Synthetics, with milk yield continuing to increase until at least 6 years of age. However, the difference is most likely the result of selection within the Synthetic dams. Increasing population size had allowed for some culling of 5-year-old dams on progeny performance in the Synthetic population. Thus the increased growth of calves of 6+-year-old dams may be an indication that selection of dams on progeny preweaning performance has been effective. If this hypothesis is true, adjustments for age of dam in the Synthetic population will be biased upward slightly.

The effect of birth weight was significant ($P<.01$) on both preweaning ADG and weaning weight. For each 1.0 kg increase in birth weight an increase of 6.7 g/day in preweaning ADG and 2.2 kg in weaning weight was observed. The genes affecting preweaning growth are probably also associated with prenatal growth and selection for increased preweaning growth would also be expected to increase birth weight.

Postweaning traits

Mean squares from the analyses of variance for postweaning ADG and yearling weight in males and 18-month weight in females are shown in Table 4.7 and least squares means with standard errors within breed and age of dam in Table 4.8. There were significant($P<.05$) breed differences with Synthetic males gaining 108.9 g/day more than the Hereford males and weighing 54.6 kg more at one year of age. Synthetic females outweighed the Hereford females by 33.7 kg at 18 months of age. Age of dam affected only yearling weight of males and 18-month weight of females. It can be concluded that there is no age of dam effect on postweaning growth. The differences present in end point weights reflect the remaining influence of age of dam on preweaning growth characteristics. Some authors have reported compensatory postweaning growth in progeny from 2- and 3-year-old dams (Pabst *et al.* 1977). In this study, no compensatory growth was apparent since the weight differences between age of dam subclasses at weaning were not diminished at a year of age.

The significant breed x year interaction in postweaning ADG ($P<.01$) and yearling weight ($P<.05$) suggest differences in growth between breeds over years. Much of this interaction may be attributed to a differential response to selection for postweaning growth in the two populations.

Table 4.7. Analyses of variance for postweaning ADG and yearling weight in males and 18-month weight in females.

Source	Means Squares: Males df	Postweaning ADG (kg)	Yearling Weight (kg)	Females df	18 month weight (kg)
Breed (B)	1	5.024**	1262878.46**	1	473201.40**
Age of Dam (A)	2	.030	74090.76**	2	79822.29**
BA	2	.035	10311.55	2	3750.93
Years (Y)	12	5.048**	201109.81**	15	44344.54**
BY	12	.371*	20852.88**	15	2225.31
Residual	962	.072	4783.71	1169	2327.18

* P<.05
**P<.01

Adjustment Factors for Preweaning Traits

The existence of the significant (P<.05) sex of calf x age of dam interaction for preweaning ADG and weaning weight, demands that these traits be adjusted for age of dam within sex. However, the absence of any 2- or 3-way interactions involving breed, sex of calf or age of dam for birth weight suggests that adjustments for this trait may be calculated across breeds and sexes.

Since age of dam adjustments for preweaning traits are made to the basis of a 6+-year-old dam, the additive factors are simply the deviations of each age of dam subgroup (Table

Table 4.8. Least squares means and standard errors of Hereford and Synthetic postweaning ADG, yearling weight and 18 month weight data.

Age of Dam (yr)	Postweaning[1] ADG (g /day)	Hereford Yearling[1] Weight (kg)	18 month[2] Weight (kg)
2	1340 ± 20	416.6 ± 5.3	342.9 ± 3.3
3	1322 ± 23	417.6 ± 6.1	350.5 ± 4.0
4+	1336 ± 13	436.4 ± 3.4	365.7 ± 2.0
Age of Dam Pooled	1334 ± 10	428.7 ± 2.7	353.0 ± 1.9
		Synthetic	
2	1421 ± 16	456.9 ± 4.1	377.8 ± 2.6
3	1450 ± 17	477.5 ± 4.3	387.8 ± 2.7
4+	1447 ± 9	494.1 ± 2.5	394.4 ± 1.6
Age of Dam Pooled	1443 ± 7	483.3 ± 1.9	386.7 ± 1.4

[1] Males only: years 1966-1978
[2] Females only: years 1962-1977

4.9). Multiplicative adjustment factors are computed by dividing the least squares means of the 6+-year-old subgroup by each of the other age of dam subgroups (Table 4.10).

In order to be effective, adjustment factors must equalize both means and variances of each age of dam subgroup. Multiplicative or additive adjustments may be used. Both equalize subgroup means; however, their effects

Table 4.9. Additive age of dam adjustment factors for birth weight, preweaning ADG and weaning weight.

Age of Dam (yr)	Birth Weight (kg) Sexes Pooled	Preweaning ADG (g/day) Males	Females	Weaning Weight (kg) Males	Females
		Hereford			
2	5.7	117	149	26.5	33.0
3	3.4	100	63	21.7	14.9
4	1.8	18	42	4.7	10.1
5	.5	0	8	.3	2.7
6+	0	0	0	0	0
		Synthetic			
2	5.7	183	162	38.6	34.6
3	3.4	102	87	21.1	19.3
4	1.8	423	56	8.8	12.3
5	.5	36	35	6.2	7.4
6+	0	0	0	0	0

on subclass variances differ. If subclass variances are equal, additive adjustments should be applied since they have no effect on the variance. If variances differ in a scalar manner, with the smallest means having the smallest variances, a multiplicative adjustment will tend to equalize the variances by increasing them by the square of the factor used, if the factor is greater than 1.

Table 4.10. Multiplicative age of dam adjustments for birth weight, preweaning ADG and weaning weight (%).

Age of Dam (yr)	Birth Weight	Preweaning		Weaning Weight	
	Sexes Pooled	Males	Females	Males	Females
		Hereford			
2	1.20	1.16	1.23	1.17	1.22
3	1.11	1.13	1.08	1.13	1.09
4	1.06	1.02	1.05	1.03	1.06
5	1.02	1.00	1.01	1.00	1.02
6+	1.00	1.00	1.00	1.00	1.00
		Synthetics			
2	1.17	1.21	1.21	1.21	1.20
3	1.09	1.11	1.10	1.10	1.10
4	1.05	1.04	1.06	1.04	1.06
5	1.01	1.04	1.04	1.03	1.04
6+	1.00	1.00	1.00	1.00	1.00

Standard deviations for age of dam and sex of calf subgroups in both breeds for all preweaning traits were calculated (Table 4.11). In general the variances between age of dam subgroups were similar for any one trait within breed. The greatest differences occurred in preweaning ADG and weaning weight in Synthetics where a disproportionately large variance was found for 2-year-old dams. However, the magnitude of the variances was not scalar, and as such, a

Table 4.11 Variances of age of dam and sex within breed for birth weight, preweaning ADG and weaning weight.

Age of Dam (yr)	Birth Weight (kg)[2]	Preweaning ADG (g/day)[2]	Weaning Weight (kg)[2]
		Hereford	
2	13.6	12996	470.9
3	12.8	13924	508.5
4	12.3	12769	453.3
5	13.7	11449	417.4
6+	14.7	13924	498.2
Sex			
Males	13.9	14884	526.7
Females	13.1	11449	417.8
		Synthetic	
2	17.3	24336	984.7
3	19.3	11664	449.4
4	15.8	10404	374.0
5	18.5	11449	417.9
6+	19.6	12321	464.4
Sex			
Males	19.0	17161	668.2
Females	17.1	11236	436.4

multiplicative adjustment factor may only increase the variation in the variances. Additive factors will therefore be applied to adjust for age of dam.

Although the multiplicative age of dam adjustment factors generally increase variance differences, their similarity between breeds may justify their use in cases where many breeds are involved such as in ROP testing. Between breeds, and within sex, the differences in magnitude are seldom greater than 2.9 which may be acceptable in some programs. Work with larger populations may reveal that the differences between sexes are also smaller than those computed in the present study. In this case, one set of multiplicative age of dam adjustment factors could be computed for all breeds.

For sex of calf, the variance for females in all cases was lower than that for males. A multiplicative adjustment is the adjustment of choice for sex since when applied to the female data, it would tend to equalize the variance of females with that of the males. Table 4.12 shows the multiplicative sex adjustment factors which adjust all data to a male basis. Synthetic males exceed Synthetic females by 7.0% for all three traits while Hereford males exceed Hereford females by 6.0% for birth weight and 5.0% for preweaning ADG and weaning weight.

The adjustment factors for Hereford males compare favorably with previous estimates in the literature (Sellers 1968; Schaeffer and Wilton 1974). Those for Hereford females

Table 4.12. Multiplicative adjustment factors for sex breed for birthweight, preweaning ADG and weaning weight.

Breed and Sex	Birth Weight	Preweaning ADG	Weaning Weight
Hereford			
Male	1.00	1.00	1.00
Female	1.06	1.05	1.05
Synthetic			
Male	1.00	1.00	1.00
Female	1.07	1.07	1.07

on the other hand tended to be higher. This increase for Hereford females may relate to the inability of the Hereford dams to fulfil the nutritional requirements of male calves while those of females are fulfilled and a female calf from a mature dam is able to express her growth potential more fully than a male calf. This would result in larger deviations in the females than the males.

The adjustment factors for preweaning ADG and weaning weight in Synthetics are generally higher than those of the Herefords. The factors were similar in both traits.

Application of the Preweaning Adjustment Factors

Although many adjustment factors have been reported in the literature, very little has been said about the mode of application when both additive and multiplicative

adjustments are being made for age of dam and sex of calf. Anderson and Wilham (1978) suggested that when adjusting for sex and age of dam within sex of calf, the additive age of dam adjustments should be applied first, followed by the multiplicative sex of calf adjustment. Results from this method would differ from those if the multiplicative sex of calf adjustment were applied before the additive age of dam correction since in the former sequence the raw data as well as the age of dam adjustment would be adjusted for sex of calf.

Schaeffer and Wilton (1974) stated that for adjustment factors to be effective, they must not only remove the main effects, but also any interaction involving the main effects.

The adjustment factors derived in this study were tested under 3 methods of application: a) adjusting for age of dam within sex of calf (A/S), b) adjusting for age of dam within sex of calf, followed by the sex of calf adjustment (A/S:S), c) adjusting for sex of calf followed by the age of dam adjustment within sex of calf (S:A/S). Calculations were made of mean squares of sex of calf, age of dam and sex of calf x age of dam interaction of the raw data and after adjusting according to the three methods (Table 4.13).

The A/S adjustment, as expected, eliminated most of the age of dam effects while not greatly affecting the sex of calf effects. The sex of calf x age of dam interaction was also reduced. The A/S:S adjustment reduced the mean square

Table 4.13. Mean Squares of hypotheses tests for three methods of adjustment factor application (kg').

		Synthetic			Hereford		
Method*	Source	BW	ADG	WW	BW	ADG	WW
Unadjusted	Sex	2726.26	1.336	8766.28	894.01	.297	16382.66
	Age Dam	1393.26	1.424	63212.05	1052.19	.632	30730.39
	Interaction	58.79	.019	783.88	14.52	.047	1774.71
A/S	Sex	1846.24	2.084	90480.40	542.89	.206	10914.37
	Age Dam	40.59	.053	2218.66	19.99	.026	1013.99
	Interaction	24.53	.005	190.59	1.89	.003	108.71
A/S:S	Sex	145.41	.001	1426.01	131.29	.020	369.51
	Age Dam	42.59	.057	1059.16	21.10	.027	2399.92
	Interaction	25.33	.005	108.89	1.825	.003	221.43
S:A/S	Sex	70.21	.005	8.01	77.66	.001	798.24
	Age Dam	28.79	.047	1926.50	11.86	.023	855.08
	Interaction	29.65	.003	178.84	4.59	.003	116.52

*A/S = age of dam within sex;
A/S:S = age of dam within sex adjustment followed by sex adjustment;
S:A/S = sex adjustment followed by age of dam within sex adjustment

for sex of calf in all cases and further reduced the age of dam and interaction mean squares for weaning weight in the Synthetics. However, in the Herefords the mean squares of age of dam and interaction were increased. Both, however, were still well below those of the unadjusted data. The S:A/S method further reduced the sex of calf mean square for most traits. The age of dam mean squares were likewise reduced further except in the case of weaning weight in the Synthetics, where an increase is noted. This method reduced the interaction mean square for preweaning ADG in both breeds as well as the weaning weight mean square in the Herefords. The mean squares for birth weight and weaning weight in the Synthetics were increased as well as the mean square for birth weight in the Herefords.

In general, the results indicate that the S:A/S adjustment most efficiently adjusted the data, applying the calculated correction factors. Thus, the multiplicative sex of calf adjustment will be applied first, followed by the additive age of dam adjustment.

Adjustment Factors for Postweaning Traits

Since postweaning traits were analysed within sex, only age of dam adjustments were applicable. Both additive and multiplicative adjustment factors for male yearling weight and female 18-month weight are shown in Table 4.14. Since numbers of observations in age of dam subgroups were relatively low, adjustments may not be very useful in drawing conclusions about the populations. The small

Table 4.14. Additive and multiplicative age of dam adjustment factors for male yearling weight and female 18-month weight.

Age of Dam (yr)	Yearling Weight		18 month weight	
	Add. (kg)	Mult.	Add. (kg)	Mult.
		Hereford		
2	19.83	1.05	22.85	1.07
3	18.84	1.05	15.19	1.04
4+	0	1.00	0	1.00
		Synthetic		
2	37.20	1.08	16.60	1.04
3	16.59	1.03	6.60	1.02
4+	0	1.00	0	1.00

difference in the yearling adjustment between a 2- and 3-year-old dam was already evident in the weaning weight analysis and reflects the nutritional stresses experienced by male calves from Hereford 3-year-old dams. Synthetic additive factors for yearling weight correspond fairly well with those for weaning weight calculated previously. Female additive adjustments are also basically a reflection of preweaning growth.

Multiplicative factors shown exhibit some variation which might limit their usefulness. For purposes of this study, the additive adjustments were applied.

V. Selection and the Expected Genetic Response

A. Introduction

In a population where selection has been practised the changes in population means over a certain length of time are of interest. This *response* to selection is defined by Falconer (1960) as, "the difference of mean phenotypic value between the offspring of the selected parents and the whole of the parental generation before selection". Several factors influence the degree and rate of change which may be expected under selection. These include the intensity of selection, or selection differential (I) and the heritability (h^2) of the trait selected. The response to selection (R) can be predicted by combining these factors into the following equation:

$$R = h^2 I$$

The accuracy of this equation rests on obtaining a reliable estimate of h^2. Since h^2 estimates are extremely variable, the expected responses obtained by using the formula can be used only as general guidelines.

Another factor determining the rate of genetic change over time is the generation interval (M), defined as the average age of the parents when their offspring are born (Warwick and Legates 1979). Hence the measure of genetic improvement per unit of time (G_t) becomes:

$$Gt = (h^2I)/M$$

The purpose of this section will be to estimate heritabilities and selection differentials of pre-and postweaning traits studied in the two populations of beef cattle. Estimates of expected genetic response will be calculated from these parameters.

B. Materials and Methods

Heritabilities of all pre- and postweaning traits examined were estimated from variance components. Using methods described by Hazel (1943) the estimates of the "between sire" component (V(s)) and the "within sire" component of variance (V(e)) were used in the following formula to compute the heritabilities:

$$h^2 = 4V(s)/(V(s) + V(e))$$

Variance components were estimated within breeds using the MINQUE (Minimum Norm Quadratic Unbiased Estimation) method as described by Rao (1971). The mixed linear model used in the derivations was:

$$Yijkl = U + Ti + Gj + Sk(j) + Eijkl$$

where

Yijkl = an observed pre- or postweaning trait on a calf born in the *i*th year of a sire in the *j*th genetic group of the *k*th sire.

U = overall mean of all animals in the breed.

T*i* = the effect common to calves born in the *i*th year.

G*j* = the effect common to calves of sires in the *j*th genetic group.

S*k*(*j*) = a random sire effect of the *k*th sire nested within the *j*th genetic group.

E*ijkl* = a random error effect associated with each observation.

With S and e having mean zero and variances V(s) and V(e) respectively.

Selection differentials were accumulated over years using a method described by Newman *et al.* (1973). The method involved the following factors: *CG (Contemporary Group)* - a group of calves of the same sex born in the same breed and year; *ID (Individual's Deviation)* - the individual's deviation from the mean of his CG; *IAS (Individual's Accumulated Selection Differential* - the individual's ID plus the MAS (see below) of the parents of his CG; *MAS (Mean Accumulated Selection Differential)* - the weighted mean IAS of the parents of a CG (weighted by the number of progeny each parent contributed to the CG).

All foundation animals (i.e., those born prior to 1966) were arbitrarily assigned an IAS of 0. For each animal born subsequently an IAS was computed as outlined above.

For preweaning data, the contribution to the selection differential of sires and dams was estimated separately as well as each of their contributions through sons or

daughters. As data existed only for males for postweaning ADG and yearling weight, only the contribution of sires to sons and daughters could be calculated; which would be expected to include most of the selection applied in these traits. Female 18-month weight data existed only for females so the selection differential was calculated through dams to sons and daughters. This estimation would be expected to be much lower than the actual selection pressure applied since selection for increased growth in the males would also result in increased growth in females.

Mean accumulated selection differentials (MAS) realized through sires became greater than zero only in 1968 since the sires born in 1966 or later began producing progeny in that year. The MAS realized through dams appeared a year later in 1969 since no dams born in 1966 were introduced into the breeding populations. The regression of MAS on years was an estimate of the mean selection differential per year. Since it would be meaningless to include years where only foundation animals were producing, the MAS/year estimates included years 1968-1978 in males and years 1969-1978 in females.

C. Results and Discussion

Heritabilities

The heritabilities of pre- and postweaning traits are shown in Table 5.1. Values for all 3 preweaning traits were higher in the Synthetic population than those in the

Table 5.1. Heritabilities and standard errors of the pre- and postweaning traits in the Hereford and Synthetic populations.

Traits	Hereford	Synthetic
Preweaning traits		
Birth weight	.36 ± .02	.47 ± .01
Preweaning ADG	.09 ± .00	.28 ± .01
Weaning weight	.13 ± .01	.25 ± .01
Postweaning traits		
Postweaning ADG[1]	.54 ± .06	.50 ± .03
Yearling weight[1]	.42 ± .06	.45 ± .03
18-month weight[2]	.76 ± .07	.71 ± .03

[1] Males only

[2] Females only

Hereford population. Preston and Willis (1974), in reviewing the heritability estimates reported in the literature, obtained values of 0.38, 0.27 and 0.30 as average estimates for birth weight, preweaning ADG and weaning weight respectively. In the present study, birth weight estimates for both Herefords and Synthetics were near the average; however, the Herefords had much lower than average estimates for preweaning ADG and weaning weight.

Various workers (Miquel and Cartwright 1963; Dunn *et al*. 1968), in comparing the heritabilities of preweaning

traits between purebred and crossbred beef populations, have found no differences. Results in this study showed that under the existing conditions, the crossbred Synthetic population had higher heritability estimates for preweaning traits than the Hereford population. Selection for preweaning traits would be expected to be more effective in the Synthetics.

The heritability estimates for all postweaning traits were similar in both breeds. Estimates for postweaning ADG were similar to the average of .52 reported by Preston and Willis (1974). Those for yearling weight, however, were considerably lower than the reported average of .70. Dunn *et al*. (1968) reported a heritability estimate of 1.00 for 550-day weight in heifers. Thus the estimates of .76 and .71 seen in Hereford and Synthetic heifers seem reasonable.

Mean Accumulated Selection Differentials

Mean accumulated selection differentials for birth weight, preweaning ADG and weaning weight in the Herefords are tabulated in Tables 5.1*a*, *b* and *c*, while those for the Synthetics are shown in Tables 5.2*a*, *b* and *c*. Almost no selection pressure through dams for any of the traits existed since dams were selected almost entirely on reproductive performance.

The MAS realized through sires for preweaning ADG and weaning weight in the Synthetic population was 64.2 ± 6.4 g/day/year and 14.1 ± 1.2 kg/year respectively as compared to 58.5 ± 4.7 g/day/year and 10.3 ± 1.0 kg/year realized in

Table 5.1*a*. Mean accumulated selection differentials (MAS) for birth weight realized through sires and dams producing progeny in the Hereford population.

	MAS(kg) realized through:					
	Sires			Dams		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	2.0	2.0	2.0			
1969	2.6	2.5	2.5	-0.1	0.3	0.1
1970	3.5	3.7	3.6	0.4	0.3	0.4
1971	4.8	5.2	5.0	0.3	0.0	0.2
1972	8.7	8.9	8.8	0.8	-0.3	0.3
1973	7.4	8.1	7.8	0.5	0.4	0.5
1974	3.8	7.1	5.4	0.5	-0.2	0.2
1975	8.9	7.9	8.4	0.1	0.3	0.2
1976	5.1	6.9	6.0	0.2	1.0	0.6
1977	9.1	8.3	8.7	0.3	0.0	0.2
1978	5.3	6.9	6.1	1.2	0.3	0.8
bmas/yr			0.5±0.2			0.1±0.0

Table 5.1*b*. Mean accumulated selection differentials (MAS) for preweaning ADG realized through sires and dams producing progeny in the Hereford population.

	MAS(gm/day) realized through:					
	Sires			Dams		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	52.4	20.0	36.2			
1969	118.7	119.1	119.4	-1.0	12.5	5.8
1970	148.3	134.8	141.6	10.0	2.4	6.2
1971	209.2	233.4	221.3	-4.0	13.0	4.5
1972	251.0	227.5	239.3	10.0	16.0	13.0
1973	341.0	352.6	347.3	3.0	41.0	22.0
1974	275.5	352.7	314.6	21.0	-8.0	6.5
1975	543.4	532.2	538.3	16.0	-9.8	3.1
1976	400.7	481.1	440.4	-8.0	1.5	-3.3
1977	603.9	598.4	601.7	24.7	-0.9	11.9
1978	548.8	684.3	616.6	22.4	9.4	15.9
bmas/yr			58.5±4.7			0.3±0.8

Table 5.1*c*. Mean accumulated selection differentials (MAS) for weaning weight realized through sires and dams producing progeny in the Hereford population.

	MAS(kg) realized through:					
	Sires			Dams		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	11.3	5.6	8.5			
1969	23.7	23.9	23.8	-0.7	2.5	-0.9
1970	30.3	29.7	30.0	1.6	0.6	1.1
1971	42.2	47.1	44.7	-0.7	2.3	0.8
1972	55.1	51.0	53.0	2.3	2.5	2.4
1973	68.7	71.5	70.1	0.8	2.5	1.7
1974	48.8	70.4	59.6	3.9	-1.7	1.1
1975	106.7	106.3	106.5	2.6	-0.1	1.3
1976	76.0	98.5	81.3	1.3	1.9	1.6
1977	112.2	108.4	110.3	5.7	0.4	3.1
1978	96.0	113.3	104.6	2.5	2.4	2.5
bmas/yr			10.3±1.0			0.3±0.9

the Hereford population. Since approximately the same proportion of sires were selected each year in each population, a greater amount of variation in the Synthetics was likely responsible for the larger selection differential in this population. In spite of attempts to avoid selecting animals with excessive birth weights, positive MAS values for birth weight were realized through sires in both populations. An increased MAS of 1.6 ± 0.3 kg/year was seen for birth weight in the Synthetic population compared with 0.5 ± 0.2 kg/year in the Hereford population.

Mean accumulated selection differentials realized through sires for postweaning ADG and yearling weight are given in Tables 5.3*a* and *b*.

Table 5.2*a*. Mean accumulated selection differentials (MAS) for birth weight realized through sires and dams producing progeny in the Synthetic population.

	MAS(kg) realized through:					
	Sires			Dams		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	4.0	4.9	4.5			
1969	5.6	5.5	5.5	-0.4	0.3	-0.1
1970	4.5	6.2	5.4	-0.2	-0.5	-0.3
1971	5.9	7.1	6.5	0.2	0.4	0.3
1972	16.0	16.0	16.0	-0.2	-0.5	-0.3
1973	8.3	9.6	8.9	-0.6	-0.8	-0.7
1974	16.5	17.4	17.0	-0.3	-0.7	-0.5
1975	13.8	15.6	14.7	-0.7	-0.3	-0.5
1976	18.9	18.4	18.6	0.2	-0.6	-0.2
1977	13.4	15.9	14.7	0.4	-0.8	-0.2
1978	22.0	21.3	21.7	0.2	-1.0	-0.4
bmas/yr			1.6±0.3			-0.3±0.0

Table 5.2*b*. Mean accumulated selection differentials (MAS) for preweaning ADG realized through sires and dams producing progeny in the Synthetic population.

	MAS(gm/day) realized through:					
	Sires			Dams		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	68.2	83.4	75.8			
1969	84.5	123.6	104.1	4.0	24.3	14.2
1970	192.7	215.1	204.4	7.7	10.9	9.3
1971	160.1	213.3	187.2	6.1	16.4	11.3
1972	293.3	322.8	308.1	11.2	6.1	8.7
1973	328.8	391.2	360.0	-4.8	18.6	6.9
1974	662.2	449.7	556.5	53.7	-8.0	22.9
1975	464.5	464.5	464.5	5.7	21.3	13.5
1976	720.6	568.4	644.5	19.4	14.9	17.2
1977	550.0	541.1	545.6	24.4	28.1	26.3
1978	784.4	615.6	700.0	40.6	26.1	33.4
bmas/yr			64.2±6.4			2.1±0.7

Table 5.2c. Mean accumulated selection differentials (MAS) for weaning weight realized through sires and dams producing progeny in the Synthetic population.

	MAS(kg) realized through:					
	Sires			Dams		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	26.1	29.2	27.7			
1969	15.2	27.4	21.3	0.3	4.7	2.5
1970	57.6	63.4	60.5	1.6	1.5	1.6
1971	46.9	58.0	52.5	1.3	2.9	2.1
1972	95.3	107.1	101.2	1.7	0.9	1.3
1973	81.1	100.0	90.6	-1.1	3.4	1.2
1974	119.2	126.2	122.7	9.9	-1.4	4.3
1975	112.4	132.5	122.5	2.7	3.5	3.1
1976	137.4	146.8	142.1	1.7	2.9	2.3
1977	126.1	146.7	136.4	4.7	3.3	4.0
1978	157.9	170.3	164.1	7.8	3.2	5.5
bmas/yr			14.1±1.2			0.3±0.1

Table 5.3a. Mean accumulated selection differentials (MAS) for postweaning ADG realized through sires producing progeny in the Hereford and Synthetic populations.

HEREFORD.....				SYNTHETIC		
	MAS(gm/day) realized through:					
	sires			sires		
Year	to Sons	to Daughters	Avg	to Sons	to Daughters	Avg
1968	132.2	98.6	115.4	135.6	164.4	150.0
1969	140.6	129.7	135.2	131.2	172.3	151.8
1970	199.6	216.4	208.4	301.4	322.6	312.0
1971	293.1	202.1	247.6	309.5	353.7	331.6
1972	362.5	365.3	363.9	438.7	495.2	466.9
1973	509.8	439.7	474.8	479.6	489.6	484.6
1974	402.1	505.6	453.9	636.2	692.4	664.3
1975	661.3	604.2	632.8	787.6	800.6	794.1
1976	567.7	603.9	585.8	839.1	874.1	856.6
1977	614.4	698.6	656.5	936.6	972.3	954.5
1978	807.6	768.1	787.9	1042.2	1109.5	1075.9
bmas/yr			67.7±4.1			93.3±4.1

Table 5.3*b*. Mean accumulated selection differentials (MAS) for yearling weight realized through sires producing progeny in the Hereford and Synthetic populations.

HEREFORD.....SYNTHETIC

MAS(kg) realized through:

	sires			sires		
Year	to sons	to daughters	Avg	to sons	to daughters	Avg
1968	35.3	24.9	30.1	38.4	49.2	43.8
1969	47.5	44.7	46.1	42.0	56.4	49.2
1970	54.0	67.3	60.7	81.5	91.8	86.7
1971	173.5	87.7	130.6	86.3	104.7	95.5
1972	83.6	116.7	100.2	127.5	142.6	135.1
1973	220.3	153.5	186.9	146.8	161.7	154.3
1974	114.0	162.3	138.2	181.4	215.2	198.3
1975	267.2	212.2	239.7	232.5	215.6	224.1
1976	174.1	202.0	188.6	242.0	264.2	253.1
1977	282.6	244.3	263.5	268.9	260.3	264.6
1978	316.5	211.9	264.2	313.4	318.2	315.8
bmas/yr			24.4±2.8			27.6±1.0

Table 5.4 shows the MAS realized through dams for 18-month weight in the Hereford and Synthetic populations. The small positive differentials of 0.6 ± 0.2 and 0.4 ± 0.1 kg/year realized in the Herefords and Synthetics respectively were not of great significance. If there was a tendency toward increasing dam size, it may have been realized through sires to daughters with faster growing sires tending also to produce faster growing daughters. The MAS values for 18-month weight would indicate a tendency for the average sized dam to enter the breeding herd. There was no excess of small or large females being selected on reproductive performance.

Table 5.4. Mean accumulated selection differentials (MAS) for 18-month weight realized through dams producing progeny in the Hereford and Synthetic populations.

	HEREFORD			SYNTHETIC		
	MAS(kg) realized through:					
	dams			dams		
Year	to sons	to daughters	Avg	to sons	to daughters	Avg
1968	0.0	0.0	0.0	0.0	0.0	0.0
1969	1.1	5.0	3.1	5.6	7.7	6.7
1970	4.3	3.3	3.8	7.3	1.9	4.6
1971	-0.9	5.8	2.4	5.9	5.7	5.8
1972	5.8	0.5	3.1	10.7	1.3	6.0
1973	4.3	6.4	5.4	5.0	5.5	5.2
1974	1.5	6.6	4.1	7.3	2.7	5.0
1975	4.7	4.6	4.7	7.8	4.8	6.3
1976	6.0	12.3	9.2	9.1	7.7	8.4
1977	7.2	8.3	7.8	8.5	10.5	9.5
1978	8.0	7.1	7.6	7.0	11.0	9.0
bmas/yr			0.6±0.2			0.4±0.1

Expected Genetic Response

The age of parents when their offspring are born and mean selection differentials per generation and per year for preweaning traits are tabulated in Table 5.5. The average generation interval in the Hereford population of 3.75 years was longer than the interval of 3.43 years in the Synthetic population. In the years prior to 1970, the average age of dams in Herefords tended to be slightly higher than in Synthetics due to a lower number of replacement females entering the breeding herd. However, since this date, no great difference in dam age existed between the populations. In sires there was a continuing tendency to use a greater proportion of 3-year-old sires in the Herefords than in the Synthetics.

Table 5.5 Age of parents and mean selection differentials for birth weight, preweaning ADG and weaning weight in the Hereford and Synthetic populations.

Item	Hereford	Synthetic
Age sires (yr)	2.68	2.32
Age dams (yr)	4.81	4.54
Avg age parents (yr)	3.75	3.43
Mean selection differential per generation		
Birth weight (kg)	1.1	2.7
Preweaning ADG (g/day)	110.3	113.9
Weaning weight (kg)	19.9	24.7
Mean selection differential per year		
Birth weight (kg)	.3	.8
Preweaning ADG (g/day)	29.4	33.2
Weaning weight (kg)	5.3	7.2

Mean selection differentials were higher in Synthetics than in Herefords for all preweaning traits. This was also true for postweaning traits shown in Table 5.6.

Table 5.7 shows estimates of genetic responses that may be expected in the 2 populations, considering heritabilies and selection applied for the pre- and postweaning traits. Due to lower selection differentials as well as lower heritability estimates, expected gains were lower in the Herefords than the Synthetics for all traits except 18-month weight in females. Differences in expected response were greatest for preweaning traits with those for postweaning

Table 5.6. Age of parents and mean selection differentials for postweaning ADG and yearling weight of males and 18-month weight of females in the Hereford and Synthetic populations.

Item	Hereford	Synthetic
Age sires (yr)	2.68	2.32
Age dams (yr)	4.81	4.54
Avg age parents (yr)	3.75	3.43
Mean selection differential per generation		
Postweaning ADG (g/day)[1]	127.1	160.0
Yearling weight (kg)[1]	45.8	47.4
18-month weight (kg)[2]	1.2	0.7
Mean selection differential per year		
Postweaning ADG (g/day)[1]	33.9	46.7
Yearling weight (kg)[1]	12.2	13.8
18-month weight (kg)[2]	0.3	0.2

[1] Includes males only

[2] Includes females only

traits being considerably smaller. These estimates may be used only as guidelines as to the direction in which the real response should go.

Table 5.7. Estimates of expected response for preweaning and postweaning traits in the Hereford and Synthetic population.

Expected response for:	Hereford	Synthetic
Birth weight (kg)		
per generation	0.40	1.27
per year	0.11	0.38
Preweaning ADG (g/day)		
per generation	9.93	31.89
per year	2.65	9.30
Weaning weight (kg)		
per generation	2.59	6.18
per year	0.69	1.80
Postweaning ADG (g/day)		
per generation	68.6	80.0
per year	18.3	23.4
Yearling weight (kg)		
per generation	19.2	21.3
per year	5.1	6.2
18-month weight (kg)		
per generation	0.88	0.50
per year	0.23	0.14

VI. Estimation of Genetic Response to Selection

A. Introduction

Since both genetic and environmental factors influence the performance of an animal, phenotypic trends may not be totally accurate in estimating genetic responses to selection within a population. Therefore, attempts were made to separate phenotypic changes into there respective genetic

and environmental components. This section deals with 3 techniques of estimating genetic and environmental trends.

B. Estimation of Genetic Response using a Control Population

Intoduction

One possible method of measuring genetic change is comparing the selected population to a control population whose breeding value remains stable from generation to generation. Any variation over time in this control population can therefore be attributed to environmental factors.

Literature Review

Control populations have been widely used in selection experiments involving laboratory animals, such as Drosophila (Clayton *et al*. 1957), mice and rats (Bailey *et al*. 1971). The Ottawa Control and the Cornell Control are examples of established control populations in egg-type poultry. Several controls have also been established and used in turkey breeding (McCartney 1964).

Less use of control populations has occurred in large animal experiments due to the great expense of facilities and animals needed.

Studies have been reported where control populations were used in pigs (Hetzer and Harvey 1967; Edwards *et al*. 1971) and sheep (Turner *et al*. 1968). In cattle, very few experiments have been reported where environmental trends are estimated by the maintenance of a control population. A

brief description of a control herd for dairy cattle has been given by Legates and Meyers (1966) while in beef cattle, Newman *et al*. (1973) featured a control population in measuring environmental change in a selection experiment.

To be effective, a control population must remain genetically stable from generation to generation. In a review, Hill (1972) lists several ways in which a control population could change genetically and lose its effectiveness. These include: random genetic drift of the control, directional change of the control through natural or unintentional selection, interaction between the environment and the genotypes of the control or selected populations, and finally, error of estimation of the control population mean through measuring too few individuals.

The problem of small population size is common to most control populations in large animal breeding. This contributes to the chance of genetic drift as well as the error of estimation. In an idealized random mating population with discrete generations, and a random distribution of family sizes with no differential viability or fertility between families, the drift variance V(a) in a single generation is:

$$V(a)=V(g)/N \qquad \text{(Hill, 1972)}$$

where V(g) is the additive genetic variance and N the number

of individuals. As N increases, the drift decreases.

Maintaining a zero selection differential is a method commonly employed to minimize genetic drift as well as reduce the possibility of unintentional selection (Turner *et al*. 1968; Newman *et al*. 1973). In this situation, the individuals retained for breeding are chosen such that their mean performance for some particular trait is close to the mean performance of all recorded individuals in that generation.

To minimize genotype-environment interactions, the control population should be genetically similar and be subject to the same environment as the selected population. In most cases the control and selected populations originate from the same base population. Over time, due to selection in the selected population, genetic difference may occur between the two which could lead to genetic-environment interactions; however, these are normally assumed to be minimal.

Materials and Methods

The Data

The control population in the present experiment is a herd of beef cattle referred to as the Cripple population. Animals in this population are carriers or suspect carriers of arthrogyposis which is a genetic condition affecting the limbs as well as palate development. The condition was introduced from the Charolais breed where studies indicate the defect to be caused by the action of an autosomal

recessive gene showing incomplete penetrance (Goonewardene and Berg 1976). Expressivity is variable from the most severe case where all limbs are affected to cases where no visible symptoms exist.

The cripple population originated in 1966 from the Synthetic herd. As soon as a dam gave birth to a crippled calf she was removed from the Synthetic population and entered into the cripple population. The mating system practised within the population was to mate known and suspect carriers in series of planned matings in order to establish the mode of inheritance of arthrogryposis. Thus in respect to production traits, mating was random. Number of observations with data in each year from 1970 to 1978 are presented in Table 6.1.

Adjusting the Data

The preweaning data was adjusted for sex of calf and age of dam effects. Adjustments were made within age of dam and sex except for birth weight where the sexes were pooled. Multiplicative adjustments were applied for sex of calf, followed by additive adjustments for age of dam. All adjusting was to a basis of a male calf from a 6+-year-old dam. As done previously for Hereford and Synthetic data, adjustment factors were derived from the least square means of age of dam and sex of calf effects for preweaning traits and are shown in Table 6.2. Adjustment factors for age of dam were derived by changing the sign of the deviation of means from the mean of the 6+-year-old subgroup. The sex

Table 6.1 Distribution of observations by year for preweaning and postweaning traits in the control population.

Year	Preweaning Traits		Postweaning Traits	
	Males	Females	Males	Females
1970	6	2	-	2
1971	12	19	-	13
1972	10	11	8	5
1973	7	13	5	12
1974	18	12	-	12
1975	16	10	13	10
1976	9	11	9	11
1977	10	19	10	17
1978	9	16	9	

factor was determined by dividing the mean for males with that for females (Table 6.3).

Postweaning data was adjusted using factors estimated for the Synthetic population since the number of animals with postweaning data in the control population was too low to accurately estimate the effect of age of dam. Since the control population originated from a Synthetic base, the effects in both populations should be similar.

Genetic Trends

Least squares means from the years 1970-1978 were estimated for the Hereford, Synthetic and Control

Table 6.2. Least square means and standard errors of age of dam and sex effects on birth weight, preweaning ADG and weaning weight in the control population

Age of Dam (yr)	No. Males	No. Females	Birthweight (kg) Sexes Pooled	Preweaning ADG (g/day) Male	Preweaning ADG (g/day) Female	Weaning Weight (kg) Male	Weaning Weight (kg) Female
2	12	18	29.73 ± 0.99	824 ± 39	884 ± 34	178.06 ± 7.57	188.90 ± 6.45
3	16	13	35.07 ± 1.02	899 ± 36	906 ± 38	199.57 ± 6.98	195.73 ± 7.39
4	14	19	36.13 ± 0.93	1005 ± 37	941 ± 30	218.56 ± 7.21	203.94 ± 5.92
5	9	18	37.55 ± 1.08	1012 ± 44	956 ± 34	221.28 ± 8.58	208.23 ± 6.58
6+	46	45	37.88 ± 0.56	1012 ± 20	979 ± 213	227.51 ± 3.81	212.32 ± 4.11
Sex							
Females	113		33.81 ± .63	933 ± 16		201.82 ± 3.16	
Males	97		36.74 ± .62	957 ± 16		208.99 ± 3.10	

populations using the adjusted data (Tables 6.4*a*, *b* and *c*). Control data of test ADG and 365-day weight in males were missing for 1970 and 1971 so the corresponding years in the Hereford and Synthetic data were also omitted. In addition, data of the same traits for 1974 were missing in the Control but the data for that year were included for the Herefords and Synthetics.

Regressions of phenotype on time within each breed for each trait estimated the phenotypic trend over time. The phenotypic trend in the Control population was assumed to equal the environmental trend, and was subtracted from the corresponding trends in the Hereford and Synthetic populations to yield estimates of genetic trends (Table 6.5).

Unintentional Selection

In any control population, the genetic composition can change due to natural or unintentional artificial selection. The resulting effects would be biased estimates of environmental change over time. Although any natural selection effects are difficult to determine, it is possible, in retrospect, to estimate whether any unintentional artificial selection pressures have been exerted on the population. Mean accumulative selection differential values calculated after Newman *et al*. (1973) are presented in Table 6.6. Since the standard errors of the MAS regressed on years is relatively high for all traits, the values computed can not be considered as absolute values

Table 6.4a. Least square means and standard errors of adjusted preweaning and postweaning data within breed.

Hereford

Year[1]	Birth Weight (kg)	Preweaning ADG (g/day)	Weaning Weight (kg)	Test[2] ADG (g/day)	365 Day[2] Weight (kg)	540 Day[2] Weight (kg)
1970	36.88 ± .49	864 ± 74	192.51 ± 2.62	±	±	379.93 ± 5.80
1971	35.09 ± .45	828 ± 69	184.15 ± 2.42	±	±	383.81 ± 4.92
1972	37.53 ± .51	900 ± 70	199.75 ± 2.73	1395 ± 32	450.15 ± 8.24	386.80 ± 6.33
1973	38.81 ± .48	916 ± 72	203.79 ± 2.53	1235 ± 34	425.25 ± 8.63	383.91 ± 5.12
1974	37.44 ± .54	849 ± 81	190.24 ± 2.87	1022 ± 40	372.71 ± 10.36	318.10 ± 5.69
1975	37.63 ± .50	894 ± 76	198.50 ± 2.67	1379 ± 38	444.89 ± 9.71	375.41 ± 5.34
1976	37.62 ± .55	924 ± 83	204.02 ± 2.92	1444 ± 35	466.77 ± 8.96	385.34 ± 9.88
1977	38.85 ± .50	914 ± 75	203.53 ± 2.63	1682 ± 33	508.12 ± 8.31	367.98 ± 5.39
1978	38.69 ± .60	882 ± 90	197.59 ± 3.19	1368 ± 55	443.07 ± 14.07	

[1] Year of progenies birth

[2] Males only

[3] Females only

Table 6.4b. Least square means and standard errors of adjusted preweaning and postweaning data within breed.

Synthetic

Year[1]	Birth Weight (kg)	Preweaning ADG (g/day)	Weaning Weight (kg)	Test[2] ADG (g/day)	365 Day[2] Weight (kg)	540 Day[3] Weight (kg)
1970	37.56 ± .42	1095 ± 63	234.68 ± 2.22	1364 ± 28	487.50 ± 7.25	415.88 ± 4.77
1971	38.16 ± .38	1071 ± 57	230.78 ± 2.02	1468 ± 25	495.44 ± 6.41	427.15 ± 4.17
1972	40.12 ± .39	1079 ± 59	234.19 ± 2.09	1456 ± 24	502.26 ± 6.08	415.14 ± 4.72
1973	39.88 ± .39	1149 ± 59	246.78 ± 2.07	1315 ± 24	484.25 ± 6.17	407.11 ± 4.45
1974	39.80 ± .46	1086 ± 69	235.17 ± 2.43	1908 ± 36	441.16 ± 9.32	368.10 ± 3.94
1975	41.41 ± .39	1114 ± 59	241.78 ± 2.09	1515 ± 25	519.12 ± 6.29	415.43 ± 4.52
1976	39.18 ± .38	1133 ± 58	243.07 ± 2.05	1632 ± 27	535.95 ± 6.81	422.11 ± 3.97
1977	42.45 ± .37	1096 ± 57	239.72 ± 2.00	2008 ± 24	606.98 ± 6.18	399.32 ± 4.13
1978	42.11 ± .35	1115 ± 53	242.84 ± 1.87	1680 ± 23	545.71 ± 5.79	

[1] Year of progenies birth

[2] Males only

[3] Females only

Table 6.4c. Least square means and standard errors of adjusted preweaning and postweaning data within breed.

Year[1]	Control					
	Birth Weight (kg)	Preweaning ADG (g/day)	Weaning Weight (kg)	Test[2] ADG (g/day)	365 Day[3] Weight (kg)	540 Day[3] Weight (kg)
1970	38.75 ± 2.16	1025 ± 54	225.32 ±10.58	±	±	411.57 ± 25.07
1971	39.00 ± .98	972 ± 25	216.15 ± 4.81	±	±	433.51 ± 10.41
1972	38.41 ± 1.18	1045 ± 30	228.66 ± 5.82	1440 ± 77	482.94 ± 20.08	432.85 ± 16.94
1973	38.50 ± 1.27	1034 ± 36	227.12 ± 6.19	1264 ± 96	459.70 ± 25.03	384.90 ± 10.63
1974	39.94 ± 1.02	1021 ± 26	225.85 ± 4.99	±	±	366.55 ± 10.37
1975	41.22 ± 1.09	1040 ± 27	230.69 ± 5.33	1411 ± 65	482.79 ± 16.94	407.51 ± 11.26
1976	36.82 ± 1.19	980 ± 30	215.71 ± 5.82	1343 ± 70	450.41 ± 18.29	367.38 ± 10.99
1977	40.82 ± 1.03	1000 ± 26	222.61 ± 5.03	1648 ± 67	528.87 ± 17.36	356.39 ± 8.61
1978	40.89 ± 1.16	979 ± 28	219.41 ± 5.46	1451 ± 73	486.52 ± 18.96	

[1] Year of progenies birth

[2] Males only

[3] Females only

Table 6.5. Linear regression and standard errors of preweaning and postweaning traits on year of birth for the Hereford, Synthetic and Control populations.

Trait	Phenotypic Trends			Genetic Trends	
	Hereford	Synthetic	Control	Hereford Control	Synthetic Control
Birth Weight	.29 ± .11	.51 ± .12	.22 ± .18	.06 ± .21	.28 ± .22
Preweaning ADG (g/day)[1]	5.9 ± 4.0	3.8 ± 3.3	-3.7 ± 3.6	9.7 ± 5.4	7.5 ± 4.9
Weaning Weight (kg)[1]	1.36 ± .79	1.20 ± .57	- .44 ± .72	1.80 ± 1.07	1.64 ± .92
Test ADG[2] (g/day)	44.4 ± 36.9	92.5 ± 43.1	26.8 ± 24.9	17.6 ± 44.3	65.8 ± 49.4
365 Day[3] Weight (kg)	8.58 ± 7.65	16.80 ± 7.73	4.38 ± 5.45	4.20 ± 9.39	12.42 ± 12.17
540 Day[3] Weight (kg)	-2.11 ± 3.74	-2.13 ± 2.95	-9.65 ± 3.20	7.50 ± 4.93	7.52 ± 4.36

[1] Years 1970-1978

[2] Males only; years 1972-1978

[3] Females only; years 1970-1977

Table 6.6. Mean accumulated selection differentials realized in the control population.

Year	Birth[1] Weight (kg)	Preweaning[1] ADG (kg/day)	Weaning[1] Weight (kg)	Yearling[2] Weight (kg)	Postweaning[2] (ADG) (kg/day)	540 Day[3] Weight (kg)
1973	0	0	0	0	0	- 6.9
1974	0	0	0	0	0	+ 3.4
1975	+ 3.63	- .143	+ 2.0	+ 12.9	+ .084	+ 89.1
1976	- .64	- .017	- 4.2	- 6.8	+ .005	+ 5.4
1977	+ 5.31	- .016	+ 21.5	+ 18.42	+ .050	+ 9.48
1978	+ 1.72	- .157	- 27.2	- 13.83	+ .049	
bMAS/yr[4]	.022 ± 1.401	-.004 ± .042	-6.19 ± 10.0	-5.49 ± 7.50	-.006 ± .017	3.43 ± 14.12

[1] Realized through sires producing male and female progeny.

[2] Realized through sires producing male progeny.

[3] Realized through dams producing female progeny.

[4] Linear regression of MAS on year for the period 1973-1977 in 540 day weight and 1975-1978 in all other traits.

but rather as general trends, positive or negative.

Results and Discussion

In the period of 1970-1978, the increase in birthweight in Herefords was almost entirely environmental, while the Synthetics increased genotypically at ± 0.22 kg/year, accounting for approximately half of their phenotypic change over the same time period. The Herefords exceeded the Synthetics both phenotypically and genotypically in yearly increases in preweaning growth traits during the last 9 years of the experiment. Genetic gains of 9.7 ± 5.4 g/day for preweaning average daily gain and 1.81 ± 1.08 kg for weaning weight were recorded for the Herefords, while those for the Synthetics were 7.5 ± 4.9 g/day and 1.64 ± .92 kg respectively. Although the heritability of preweaning traits is low and variable, it is difficult to explain the greater genetic gains for these traits in the Herefords than the Synthetics. While the rates of genetic change seen in the Synthetic population are similar to those expected, those in the Hereford population appear to be larger than expected. This may be due to the control population effectively removing environmental trends in the genetically similar Synthetics but failing to do so in the genetically dissimilar Herefords, suggesting that Herefords were more able to respond phenotypically to improving environmental conditions than Synthetics. This may be a reasonable assumption considering the more homogeneous genotype of the Hereford population. Under adverse environmental conditions,

they would also be expected to deteriorate phenotypically more rapidly. For postweaning traits in males during the period 1972-1978, the genetic gain in postweaning ADG was 65.8 ± 49.4 g/day in Synthetics and 17.6 ± 44.3 g/day in Herefords. The respective yearling weight gains were 12.42 ± 12.17 kg and 4.21 ± 9.40 kg. Although these estimations have large standard errors and tend to be higher than expected, they are probably fairly accurate in portraying the relative rates of response in the two populations for postweaning growth. The control population exhibited phenotypic increases of these two traits in spite of a negative MAS, suggesting that environmental factors conducive to postweaning growth have improved during the past 7 years. Environmental factors for preweaning growth have basically remained constant since the slight phenotypic decline in preweaning average daily gain and weaning weight correspond to a negative MAS over the same period.

Heifers of both breeds exhibited a similar phenotypic and genotypic trend for 540 day weight during the years 1970-1977. The genetic trend for the Herefords was 7.55 ± 4.94 kg/year while that for the Synthetics was 7.52 ± 4.36 kg/year. Phenotypic trends were negative suggesting that environmental factors have tended to reduce heifer weight over this time period. This point is reinforced in the control population where in spite of a positive MAS, 540 day weights have declined by 9.66 ± 3.21 kg/year.

C. Estimation of Genetic Response to Selection using the BLUP (Best Linear Unbiased Prediction) Method

Introduction

Sire evaluation has been an important part of genetic improvement over the past 50 years, especially in the dairy industry where artificial insemination is common and one sire may have progeny in multiple herds in different years. By making contemporary comparisons of the progeny of various sires within herd-year subgroups, the breeding values of sires can be estimated. By grouping sires into some logical genetic time periods (i.e., sire year of birth), the trend in breeding value is an estimate of the genetic trend due to sires.

The use of BLUP procedures has been restricted to the analyses of large data bases, such as ROP data.The purpose of this section will be to apply BLUP procedures to data from individual herds and attempt to estimate genetic trends from the results.

Literature Review

Best Linear Unbiased Prediction (BLUP) as developed by Henderson (1973) is considered by some to be the procedure which provides the best statistical predictors of sire genetic values. That is, no other linear unbiased procedure can provide predictors with smaller prediction error variances. Most application of this procedure has been in dairy cattle; however, with the recent increase of artifical insemination in beef cattle, evaluation of beef sires has

also become more important.

Schaeffer and Wilton (1974) employed BLUP procedures in evaluating progeny tested beef sires for 200-day weaning weight, postweaning ADG and yearling weight. Their data came from the Canadian Department of Agriculture and the Canadian Record of Performance and comprised of 145,881 records. Tong and Newman (1979) used BLUP procedures in estimating the effect of age of dam on weaning weight of beef cattle. Again, data was extensive, originating from the records of the Federal and Alberta provincial Record of Performance programs. Kennedy and Henderson (1977) analysing a total of 61,688 Hereford and 22,333 Aberdeen Angus calf growth records, used BLUP procedures to estimate annual genetic trends among sires and dams.

Materials and Methods

The preweaning data, adjusted for sex of calf and age of dam and the postweaning data adjusted for age of dam were used in this section of the study. Since the sex of calf and age of dam adjustments derived earlier from least squares means adjusted the data satisfactorily, these effects were not included in the model for the BLUP analysis. Computational costs also encouraged use of the pre-adjusted data. The following mixed model was assumed for the analysis:

$$Y_{ijkl} = U + T_i + G_j + S_{k(j)} + E_{ijkl}$$

where

Y_{ijkl} = an observation for a growth trait

U = the overall mean of the population

T_i a fixed effect common to calves born in the ith time period

G_j = a fixed effect common to calves of sires born in the jth sire group.

$S_{k(j)}$ = a random effect common to calves of the kth sire nested within the jth sire group.

E_{ijk} = a random error effect with each record.

With s and e having mean zero and variances V(s) and V(e) respectively.

All sires with less than 4 progeny were dropped from the analyses. Sire groupings were based on year of birth of the sire. To ensure an ample number of observations in each sire group, 2 years of birth of sire were combined to form one sire group.

Initial analyses revealed that sire groups and years were almost completely confounded due to the small number of sires in any sire group having progeny in 2 or more years. This necessitated combining 2 years into one time period which overlapped within 2 sire groups. Due to the lack of connectedness between the 1965 and 1966 data, the data prior to 1966 could not be included in the analyses. Also since each time period included exactly 2 years, the 1966 data was also dropped in the analyses of preweaning traits.

The following 6 sire group and 6 time period groupings were applied to the fixed effect classifications for

preweaning traits:

Sire group: 1965-66, 1967-68, 1969-70, 1971-72, 1973-74, 1975-76.

Time period: 1967-68, 1969-70, 1971-72, 1973-74, 1975-76, 1977-78.

Additional difficulties with confounding between time period and sire groups existed in the postweaning data. Since analysis was within sex the number of observations were reduced and the overlap of sire groups between time periods was further reduced as well. As an attempt to increase the degree of connectedness among sire groups, years were redistributed among time periods. With sire groups remaining the same, time period classifications were reduced to 5 groupings to become:

Time period: 1968-69, 1970-71, 1972-73, 1974-75, 1976-77.

The use of BLUP procedures requires knowledge of the variance components, V(s) and V(e). These were estimated by a procedure known as MINQUE (Minimum Norm Quadratic Unbiased Estimation) developed by Rao (1971). A computer program developed by Tong (personel communications) was used to simultaneously estimate the variance components using the MINQUE procedure and calculate the BLUP values. To more fully explain the procedure used and the relationship between MINQUE and BLUP, the model will be re-written in matrix notation.

$y = Xb + Zu + Wh + E$ where

y = the vector of observations on either preweaning or postweaning traits.

b = the vector of fixed effects analogous to time periods.

u = the vector of fixed effects analogous to sire groups.

h = the vector of random effects analogous to sires.

E = the vector of random error terms.

The matrices X, Z, and W are design matrices of zero and ones, corresponding in dimensions to the length of the vectors with which they are associated.

Now the least squares equations can be written as:

$$\begin{vmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z & Z'W \\ W'X & W'Z & W'W \end{vmatrix} \begin{vmatrix} b \\ u \\ h \end{vmatrix} = \begin{vmatrix} X'y \\ Z'y \\ W'y \end{vmatrix}$$

BLUP equations are formed by adding the V(e)/V(s) ratio to the sire by sire parts of the equations. Doing this yields the following equations:

$$\begin{vmatrix} X'X & X'Z & X'W \\ Z'X & Z'Z & Z'W \\ W'X & W'Z & W'W+IR \end{vmatrix} \begin{vmatrix} b \\ u \\ h \end{vmatrix} = \begin{vmatrix} X'y \\ Z'y \\ W'y \end{vmatrix}$$

where I is an identity matrix with 1's on the diagonal and R is the V(e)/V(s) ratio.

The MINQUE procedure used to estimate the variance components employed the same set of equations. The starting ratio was set at 1 and through an iterative process, new ratios are estimated and substituted back into the equations. Generally, within 5 rounds of iteration, the substituted ratio and the newly estimated ratio converged to be the same. Setting the constraints that u = T6 = G6 = 0, and applying the estimated V(e)/V(s) ratio, solutions to the equations were obtained. These solutions in fact, gave the BLUP values.

Since sire solutions were nested within groups, sire proofs were calculated by:

$$Ph = Gi - G6 + Sij$$

where

Gi = genetic group solutions

Sij = sire solutions.

Now an estimate of the genetic trend due to sires can be calculated, based on average weighted sire proofs. In year *k*:

$$GVk = \frac{Ph(Nhk)}{Nhk}$$

where

GV*k* = an average genetic value of cattle calving in year *k*, contributed by sires of these progeny.

N*hk* = the number of progeny of sire *h* in year *k*.

The GV estimates are deviations from the mean value of sires in the 6*th* genetic group, or sires born in 1975-76 (i.e., if the GV of calves born in year *n* is -10 kg, then their genetic value is 10 kg less than the mean of all calves born to sires of the last genetic group).

The regression of GV values on years was taken as an estimate of genetic trend due to sires during the time period studied.

Results and Discussion

Variance Components

Error and sire variance components for birth weight, preweaning ADG and weaning weight are shown in Table 6.7. Variances for the preweaning traits in Synthetics were higher than those in Herefords in all cases. Non-genetic sources of variations played a much greater role in the Hereford population when compared to the Synthetics. This

Table 6.7. Sire and error variance components for birth weight, preweaning ADG and weaning weight (kg^2)[1].

Component	Birth Weight	Preweaning ADG	Weaning Weight
		Hereford	
Sire (S)	3.1	.0008	42.1
Error (E)	32.0	.0333	1195.0
E/S	10.2	42.9	28.4
		Synthetic	
Sire (S)	5.4	.0023	73.0
Error (E)	40.6	.0303	1100.9
E/S	7.5	13.3	15.1

[1] Includes years 1967-1978.

was especially true in preweaning ADG where the sire variance was only .0008 compared to .0023 in the Synthetics.

Table 6.8 contains sire and error variances for postweaning traits in males and females. The genetic component was similar between breeds for postweaning ADG and yearling weight but higher in Herefords for 18-month weight in heifers.

Since variance components tend to vary depending on environmental or managerial practices, a wide range of estimates are reported in the literature (Dunn *et al*. 1968; Schaeffer and Wilton 1974; Kennedy and Henderson 1975)

Genetic trends

Table 6.8. Sire and error variance components for postweaning ADG and yearling weight in males and 18-month weight in females (kg[1]).

Component	Postweaning ADG[1] (kg)[2]	Yearling Weight[1] (kg)[2]	18 month weight[2] (kg)[2]
	Hereford		
Sire (S)	.0101	512.7	598.6
Error (E)	.0644	4362.1	2570.7
E/S	6.3	8.5	4.3
	Synthetic		
Sire (S)	.0108	575.6	467.0
Error (E)	.0751	4853.9	2175.8
E/S	7.0	8.0	4.7

[1] Males only; includes years 1968-1977

[2] Females only; includes years 1968-1977.

Table 6.9. Distribution of observations and BLUP estimates of yearly genetic values (GV) for birth weight, preweaning ADG and weaning weight in the Hereford population.

Year	No. of Sires	No. of Progeny	Birth Weight (kg)	Preweaning ADG (g/day)	Weaning Weight (kg)
1967	3	20	-.33	-28.2	-9.08
1968	7	51	-.77	-30.9	-7.63
1969	7	75	-.65	-44.2	-9.85
1970	7	70	-.32	-42.3	-9.10
1971	7	82	.47	-25.9	-5.31
1972	7	67	1.21	- 4.5	- .58
1973	7	82	1.35	-20.6	-2.03
1974	6	57	.78	-35.9	-5.53
1975	7	71	.39	3.4	.91
1976	8	61	.45	15.0	3.18
1977	8	76	-.07	3.9	.51
1978	5	52	-.05	- 2.4	- .54
b=GV/year			.08 ± .06	4.2 ± 1.2	1.10 ± .21

Table 6.10. Distribution of observations and BLUP estimates of yearly genetic values (GV) for birth weight, preweaning ADG and weaning weight in the Synthetic population.

Year	No. of Sires	No. of Progeny	Birth Weight (kg)	Preweaning ADG (g/day)	Weaning Weight (kg)
1967	4	42	.26	-62.7	-10.21
1968	6	76	.02	-37.6	- 6.31
1969	8	102	-.17	1.0	.66
1970	7	104	-.64	24.8	4.19
1971	8	128	-.69	28.3	5.56
1972	7	120	.48	35.9	7.84
1973	7	123	1.07	30.6	7.43
1974	7	99	1.27	-5.9	1.46
1975	7	119	1.74	31.3	7.35
1976	9	122	.55	43.6	8.61
1977	8	131	.07	3.4	.63
1978	8	147	-.01	7.8	1.24
b=GV/year			.07 ± .06	4.8 ± 2.3	.86 ± .43

Table 6.11. Distribution of observations and BLUP estimates of yearly genetic values (GV) for postweaning ADG, yearling weight and 18-month weight in the Hereford population.

Year	No. of sires	No. of progeny	Postweaning[1] ADG (g/day)	Yearling[1] weight (kg)	18-month[2] weight (kg)
1968	5	25	-598.6	-100.4	18.2
1969	7	36	-549.1	-100.4	14.6
1970	6	39	-516.4	- 96.4	14.3
1971	6	35	-510.0	- 99.4	14.0
1972	5	27	-493.2	- 99.6	9.4
1973	6	29	-616.4	-117.5	20.0
1974	5	16	-559.5	- 92.7	-38.4
1975	4	18	-195.9	- 32.4	-41.7
1976	7	25	-205.0	- 32.1	-38.8
1977	7	31	-221.9	- 3.4	- 4.5
b=GV/year			43.2 ± 12.5	10.1 ± 2.8	-6.1 ± 2.1

[1] Includes males only

[2] Includes females only

Table 6.12. Distribution of observations and BLUP estimates of yearly genetic values (GV) for postweaning ADG, yearling weight and 18-month weight in the Synthetic population.

Year	No. of sires	No. of progeny	Postweaning[1] ADG (g/day)	Yearling[1] Weight (kg)	18-month[2] Weight (kg)
1968	6	36	-800.5	-150.2	89.6
1969	8	59	-683.2	-125.3	90.5
1970	6	42	-683.6	-133.8	80.5
1971	8	54	-633.6	-131.8	103.0
1972	7	60	-631.8	-131.0	85.0
1973	7	58	-731.4	-143.8	47.5
1974	5	21	-733.6	-141.7	-6.2
1975	7	55	-401.8	- 78.2	10.1
1976	9	47	-373.6	- 69.4	22.5
1977	8	59	- 21.5	- 1.8	4.5
b=GV/year			61.7 ± 17.1	11.9 ± 3.5	-11.9 ± 2.5

[1] Includes males only

[2] Includes females only

Average genetic values of calves born in each year, regressed on years gave an estimate of the genetic trend due to sires. Tables 6.9 and 6.10 give these values for birth weight, preweaning ADG and weaning weight for the Hereford and Synthetic populations respectively.

A small positive genetic trend estimate of 0.07 to 0.08 kg/year was similar to the value of 0.11 kg/year predicted for Herefords, but less than the value of 0.38 kg/year expected in the Synthetics.

Genetic trends in preweaning ADG were similar in both populations with the rate of increase in the Synthetics exceeding that of the Herefords by only 0.60 g/day/year. The magnitude of the trend for preweaning ADG may be approximately that predicted in the Hereford population; however, the estimate for the Synthetics appears to be lower than that expected. This is also true in the genetic trends found for weaning weight where the value for Herefords exceeds that for the Synthetics.

Results for postweaning traits are shown in Tables 6.11 and 6.12 for the Hereford and Synthetic populations, respectively. Postweaning ADG increased at a rate of 43.2 ± 12.5 g/day/year in the Herefords and 61.7 ± 17.1 g/day/year in the Synthetics. Respective values for yearling weights are 10.1 ± 2.8 kg/year and 11.9 ± 3.5 kg/year. Increases in postweaning ADG are considerably higher than those expected while the estimates of yearling weight are extremely close. However, considering the fact that the phenotypic trend in

yearling weight was 3.4 kg and 8.8 kg in Herefords and Synthetics respectively, and negative environmental trends in the postweaning growth traits are highly unlikely, the genetic values estimated by the BLUP method appear to be too large.

The negative genetic trends of -6.1 ± 2.1 and -11.9 ± 2.5 for 18-month weight in Herefords and Synthetics is difficult to explain, due to the continued selection for increased growth rate in both populations.

The conclusions drawn from the present study are that the BLUP technique did not adequately separate environmental and genetic trends in the data. Standard errors of sire proof predictions were large because sire numbers as well as progeny per sire contained in each sire group-year subclass were too small. As well, for an accurate sire proof estimation, a sire must have progeny in several sire group-year subclasses so that adequate contemporary comparisons can be made of the sires progeny with that of other sires. This would almost restrict the method to artifical insemination situations where sires have many progeny in many years.

D. Estimation of Genetic Trends using Repeat Matings

Introduction

Possibly the most common technique used in estimating genetic trends in beef cattle is the repeat mating method. Since cattle have long generation intervals with overlapping

generations the method is well suited to this species. With the advent of frozen semen a sire may have progeny in 2 widely separated years. Genetic changes between these years can then be estimated. The scope of this section will be the estimation of genetic trends using repeat mating analyses.

Literature Review

The technique of separating environmental and genetic changes over years by the use of repeat matings was first introduced by Goodwin *et al.* (1960). They described a breeding plan for poultry in which a generation of progeny from the same parents or grandparents were repeated in two successive years. Smith (1962) adapted this scheme to fit field data collected from large animals. Sires, used in two or more years provide a continuity of genotypes by which genetic change could be measured. If the change in performance of a population over one year is represented by t + g, then the changes in performance of successive groups of progenies of individual sires is t + 1/2 g, assuming their mates are random samples of those available. That is, the genetic change in the population is g, the genetic change in any one sire is taken to be zero, so that the genetic change in his progeny over one year measures the genetic change in dams, or 1/2 g. The difference (t + g) - (t + 1/2 g) measures the genetic change in sires or half the genetic change in that year. Smith (1962) outlined several methods by which the genetic trends could be estimated following this principle. The rate of change can be

estimated as 2(B*pt* - B*st*) where B*pt* was the linear regression of performance on time and B*st* the pooled within-sire regression of progeny performance on time. Using means, rather than regressions, the genetic change over *y* years is given by:

$$\frac{2[(Xty - Xsy) - (Xto - Xso)]}{y}$$

where Xt and Xs are the population and repeat sire means and *o* is taken as the base year. The regression and means method are identical when any individual sire has progeny in no more than 2 years.

A related scheme of estimation of genetic change was outlined by Dickerson (1969). He described a technique of comparing contemporary progeny by sires of two different generations. Dams of each age and generation were assigned randomly to the sires of the 2 birth-year groups.

Repeat matings have been used in the limited number of cases where genetic and environmental trends have been separated in beef cattle breeding programs. Most workers (Flower *et al.* 1964; Brinks *et al.* 1965; Fahmy and Lalande 1973; Nwakalor *et al.* 1976) used full repeat matings where the same sires were mated to the same dams in 2 consecutive years. The difference between the progeny means was taken as an estimate of environmental change with the remaining phenotypic change assumed to be genetic. The genetic trend

was simply the difference between the regression of phenotypic means on years less the regression of the environmental changes on years. In addition to this, Fahmy and Lalande (1973) estimated genetic trends due to both sires and dams. They took the difference between maternal half-sib calves produced in 2 consecutive years as a measure of the environmental plus one-half of the genetic change due to sire (e + 1/2 gs). The difference between paternal half-sib calves born in 2 consecutive years was a measure of the environmental plus one-half of the genetic change due to dams (e + 1/2 gd). The genetic change per year was then estimated as [(e + 1/2gs) + (e + 1/2gd) - 2e]

The problem associated with full repeat matings is the confounding of age of dam within the estimation of environmental trends. Generally age of dam corrections are made across years and as such, the adjustment within any single year may not be exact. A method of overcoming this problem is to repeat mate only older dams where age effects are minimal. Vesely and Peters (1975) attempted this in sheep where they repeated only 3- to 5-year-old ewes. No reports were found where this has been considered in beef cattle breeding.

Materials and Methods

The Data

Approximately 8 to 10 sires were used in the Hereford and Synthetic populations each year. Of these sires, one or two were generally repeat sires which had already produced

calves in the previous year. Allocation of dams to sires was completely random each year, randomizing the dam age groups among sires as well as the newly introduced dams among sires. Since full-sib comparisons between years were not possible, trends were estimated by paternal half-sib comparisons.

Means used in the analysis were derived from the preweaning data adjusted for age of calf, age of dam and sex of calf, and the postweaning data adjusted for age of calf and age of dam. Connectedness through sires is a requirement for estimating genetic trends by the repeat mating method. The data prior to 1966 could not be connected to the post-1966 data through sufficient repeated matings and thus was dropped from the analysis. Sires with less than 3 progeny in any one of the 2 years were deleted. Sufficient repeat mating observations existed in the preweaning data to analyse genetic trends within breeds. In the postweaning data, however, insufficient observations in each population resulted in the need to pool the repeat mating data of the two populations.

Repeat Mating Analysis

The difference between the raw means of paternal half-sibs born in 2 consecutive years was used in the present study as a measure of the environmental change plus the genetic change due to dams (e + gd). In most studies previously cited, one-half of the total genetic change was credited to dams. While the genetic change in individual

dams was accepted to be as great as that in individual males, since both were progeny of the same sires in the previous generation, selection practises determined how both change over time. Since dam selection in the present populations was almost entirely on reproductive capacity, there was no pressure to retain the females superior for any particular growth trait. Thus, as a sub-population, the overall genetic change in dams could not be assumed to be one-half of the total genetic change, but may in fact be much less. This is supported by Kennedy and Henderson (1977) who found very small genetic trends in dams for pre- and postweaning growth traits. In the present work the difference between means of paternal half-sibs produced in 2 consecutive years were taken as the environmental change. This would result in a slight downward bias in the genetic trends since only the genetic change in the sires was measured.

Another possible source of bias encountered was the selection of dams on the performance of their progeny, practised in the Synthetic population. This selection resulted in a more rapid change in the female sub-population of the Synthetics and as a result, an additional downward bias in the genetic trends.

The distribution of observations, progeny means of repeated matings and environmental changes for birthweight, preweaning ADG and weaning weight for both populations are shown in Tables 6.13*a*, *b* and *c*.

Table 6.13*a*. Distribution of observations,progeny means and yearly environmental changes of birth weight for the Hereford and Synthetic populations.

Year	HEREFORD			SYNTHETIC		
	No. of observations	Progeny means of repeated matings[1] (kg)	Environmental changes (kg)	No. of observations	Progeny means of repeated matings[1] (kg)	Environmental changes (kg)
1966		34.15*a*	0.00		39.77*a*	0.00
1967	16	35.84*a*	35.45*b* 1.69	34	39.30*a*	35.28*b* -0.47
1968	11	31.75*c*	36.74*b* 1.29	19	36.11*c*	35.87*b* 0.59
1969	23	35.63*c*	37.80*d* 3.88	26	37.94*c*	36.31*d* 1.83
1970	20	38.25*e*	38.17*d* 0.37	15	37.41*e*	37.82*d* 1.51
1971	45	35.20*e*	34.23*f* -3.05	26	38.56*e*	38.72*f* 1.15
1972	26	37.64*g*	38.48*f* 4.25	7	38.25*g*	43.46*f* 4.74
1973	14	38.91*g*	39.48*h* 1.27	21	37.98*g*	38.29*h* -0.23
1974	20	38.76*i*	37.48*h* -2.00	18	40.17*i*	37.72*h* -0.57
1975	7	38.57*i*	37.84*j* -.019	18	40.57*i*	42.51*j* 0.40
1976	12	35.80*k*	38.60*j* -1.66	33	39.96*k*	40.10*j* -2.41
1977	11	38.50*k*	38.21*l* 2.70	13	43.14*k*	42.62*l* 3.18
1978	12		38.21*l* -0.35	37		41.81*l* -.074

[1]The same letters indicate means of repeated matings.

Table 6.13*b*. Distribution of observations, progeny means and yearly environmental changes of preweaning ADG for the Hereford and Synthetic populations.

Year	HEREFORD No. of observations	Progeny means of repeated matings[1] (gm/day)	Environmental changes (gm/day)	SYNTHETIC No. of observations	Progeny means of repeated matings[1] (gm/day)	Environmental changes (gm/day)
1966	889.0*a*		0.00	1034.2*a*		0.00
1967	16 784.7*a*	712.1*b*	-104.3	34 993.4*a*	952.5*b*	-40.8
1968	11 916.3*c*	979.8*b*	267.6	19 1107.2*c*	1052.3*b*	99.8
1969	23 821.0*c*	875.40*d*	-95.3	26 1061.4*c*	1084.1*d*	-45.8
1970	20 870.9*e*	875.4*d*	0.00	15 1097.7*e*	1193.0*d*	108.9
1971	45 807.4*e*	811.9*f*	-63.5	26 1043.3*e*	1120.4*f*	-54.4
1972	26 916.3*g*	902.7*f*	90.7	7 1097.7*g*	1038.7*f*	-81.6
1973	14 929.9*g*	920.8*h*	13.6	21 1147.6*g*	1134.0*h*	49.93
1974	20 839.2*i*	857.3*h*	-63.5	18 1088.6*i*	1102.2*h*	-31.8
1975	7 857.3*i*	911.7*j*	18.1	18 1088.6*i*	1106.8*j*	0.00
1976	12 920.8*k*	902.7*j*	-9.1	33 1106.8*k*	1124.9*j*	18.1
1977	11 916.3*k*	929.9*l*	-4.5	13 1138.5*k*	1115.8*l*	31.8
1978	12	902.7*l*	-27.2	37	1152.1*l*	36.3

[1]The same letters indicate means of repeated matings.

Table 6.13c. Distribution of observations, progeny means and yearly environmental changes of weaning weight for the Hereford and Synthetic populations.

Year	HEREFORD				SYNTHETIC			
	No. of observations	Progeny means of repeated matings[1] (kg)		Environmental changes (kg)	No. of observations	Progeny means of repeated matings[1] (kg)		Environmental changes (kg)
1966		194.18*a*		0.00		225.45*a*		0.00
1967	16	176.98*a*	164.06*b*	-17.21	34	217.49*a*	206.40*b*	-7.95
1968	11	196.76*c*	212.89*b*	48.83	19	235.17*c*	224.97*b*	18.57
1969	23	183.72*c*	195.24*d*	-13.04	26	228.26*c*	230.83*d*	-6.91
1970	20	195.14*e*	195.60*d*	0.55	15	234.59*e*	252.08*d*	21.25
1971	45	181.78*e*	180.44*f*	-13.36	26	226.03*e*	240.47*f*	-8.56
1972	26	202.71*g*	200.39*f*	19.94	7	235.68*g*	229.89*f*	-10.57
1973	14	206.47*g*	205.00*h*	3.76	21	244.70*g*	242.74*h*	9.02
1974	20	189.65*i*	191.85*h*	-13.15	18	235.68*i*	236.49*h*	-6.25
1975	7	192.95*i*	201.93*j*	3.30	18	236.26*i*	241.51*j*	0.58
1976	12	201.44*k*	199.15*j*	-2.78	33	238.68*k*	242.10*j*	0.59
1977	11	203.59*k*	205.65*l*	2.15	13	247.93*k*	243.34*l*	9.25
1978	12		200.90*l*	-4.75	37		249.06*l*	5.72

[1]The same letters indicate means of repeated matings.

Environmental trends were estimated by accumulating the environmental changes over years. In this manner, the environmental trend related back to the base year of 1966 to which a level of zero was assigned. Response from selection was measured as a difference, in intrayear comparisons, between the least squares means of the total population and of environmental trend.

Tables 6.14*a*, *b* and *c* show the phenotypic least squares means and standard errors, environmental trends and response from selection for birthweight, preweaning ADG and weaning weight respectively.

Distribution of observations, progeny means of repeated matings and yearly environmental changes for postweaning ADG and yearling weight for males are shown in Tables 6.15*a* and 6.15*b*. Environmental changes of the 2 populations were pooled by taking their means and cumulating them over years to obtain the pooled environmental trends. In years where repeated mating data existed for only one population, that value was assumed to be the common change for that year. Table 6.16*a* and 6.16*b* show the yearly phenotypic least squares means and standard errors, the pooled environmental trends and response to selection for postweaning ADG and yearling weight in males.

Similar analysis was carried out for 18-month weight in females where the environmental trend was also calculated on a pooled basis. Results are tabulated in Tables 6.17 and 6.18.

Table 6.14*a*. Yearly phenotypic means and standard errors,enviromental trends and genetic trends for birth weight in the Hereford and Synthetic populations (kg).

	HEREFORD			SYNTHETIC		
Year	Phenotypic mean±S.E.	Enviromental trend	Genetic response to selection	Phenotypic mean±S.E.	Enviromental trend	Genetic response to selection
1966	35.01±0.71	0.00	35.01	37.70±0.50	0.00	37.70
1967	35.88±0.53	1.69	34.19	37.37±0.47	-0.47	37.84
1968	35.04±0.55	2.97	32.07	35.64±0.49	-0.12	35.52
1969	36.14±0.49	6.86	29.28	37.75±0.43	1.96	35.79
1970	36.88±0.49	7.22	29.66	37.56±0.42	3.47	34.10
1971	35.10±0.45	4.17	30.92	38.16±0.38	2.66	35.95
1972	37.54±0.51	8.42	29.12	40.12±0.35	7.40	32.72
1973	38.81±0.48	9.69	29.13	39.88±0.39	7.38	32.51
1974	37.44±0.54	7.68	29.76	39.80±0.46	6.80	33.00
1975	37.64±0.50	7.52	30.15	41.41±0.40	7.20	34.21
1976	37.62±0.55	5.83	31.78	39.18±0.39	4.79	34.39
1977	38.85±0.49	8.53	30.32	42.45±0.38	7.97	34.48
1978	38.69±0.60	8.17	30.52	42.11±0.35	7.23	34.88
b=	0.31±0.06	0.57±0.15	-0.26±0.12	0.46±0.08	0.73±0.12	-0.27±0.10

Table 6.14*b*. Yearly phenotypic means and standard errors,enviromental trends and genetic trends for preweaning ADG the Hereford and Synthetic populations (gm/day).

	HEREFORD			SYNTHETIC		
Year	Phenotypic mean±S.E.	Enviromental trend	Genetic response to selection	Phenotypic mean±S.E.	enviromental trend	Genetic response to selection
1966	843.23±98.99	0.00	843.23	1005.16±75.30	0.00	1005.16
1967	777.91±80.29	-104.33	882.24	965.24±70.31	-40.82	1006.06
1968	935.31±83.46	163.29	772.02	1045.08±74.84	57.97	986.11
1969	833.70±73.94	68.04	765.66	1047.34±64.41	9.07	1038.27
1970	864.09±74.39	68.04	796.05	1095.43±63.05	117.93	977.50
1971	827.81±68.95	4.53	823.28	1070.48±57.15	63.50	1006.98
1972	900.83±77.56	95.25	805.58	1078.64±59.42	-18.14	1096.78
1973	916.26±72.12	108.85	807.39	1149.86±58.51	31.75	1118.11
1974	848.68±81.19	45.35	803.32	1085.90±68.95	0.00	1085.90
1975	893.58±75.75	63.49	830.09	1113.57±59.42	0.00	1113.57
1976	923.97±83.01	54.42	869.55	1133.07±58.06	18.14	1114.93
1977	914.44±74.84	49.85	864.59	1096.33±56.70	49.90	1046.43
1978	882.24±90.72	22.68	859.56	1114.93±53.07	86.18	1028.75
b=	6.08±3.06	2.84±4.84	3.25±2.72	10.57±2.37	2.82±3.35	7.76±3.25

Table 6.14c. Yearly phenotypic means and standard errors,enviromental trends and genetic trends for weaning weight in the Hereford and Synthetic populations (kg).

	HEREFORD			SYNTHETIC		
Year	Phenotypic mean±S.E.	Enviromental trend	Genetic response to selection	Phenotypic mean±S.E.	enviromental trend	Genetic response to selection
1966	186.83±3.76	0.00	186.83	218.57±2.45	0.00	218.57
1967	175.99±2.83	-17.21	193.19	211.09±2.18	-7.95	219.04
1968	203.52±2.94	31.62	171.90	226.20±2.21	10.61	213.04
1969	186.27±2.60	18.57	167.69	226.20±2.34	3.70	222.50
1970	192.51±2.62	19.13	173.38	234.68±2.18	24.95	209.73
1971	184.15±2.42	5.77	178.38	230.78±2.32	16.39	214.39
1972	199.75±2.73	25.71	174.04	234.19±2.46	5.82	228.37
1973	203.79±2.53	29.47	174.32	246.78±2.31	14.84	231.94
1974	190.24±2.87	16.32	173.93	235.17±2.65	8.59	226.59
1975	198.50±2.66	19.61	178.88	241.78±2.36	9.16	232.62
1976	204.02±2.92	16.83	187.19	243.07±2.24	9.75	233.32
1977	203.53±2.63	18.99	184.54	239.73±2.20	19.00	220.72
1978	197.59±3.19	14.23	183.36	242.84±2.19	24.72	218.12
b=	1.40±0.56	1.26±0.93	0.10±0.60	2.36±0.41	1.44±0.58	0.93±0.53

Table 6.15*a*. Distribution of observations, progeny means and yearly environmental changes of male postweaning ADG for the Hereford and Synthetic populations.

Year	HEREFORD				SYNTHETIC			
	No. of observations	Progeny means of repeated matings[1] (gm/day)		Environmental changes (gm/day)	No. of observations	Progeny means of repeated matings[1] (gm/day)		Environmental changes (gm/day)
1966		1238.3*a*		0.00		1324.5*a*		0.00
1967	7	1365.3*a*	1424.3*b*	127.0	15	1505.9*a*	1315.4*b*	181.4
1968	4	1215.6*c*	1388.0*b*	-36.3	9	1206.6*c*	1265.5*b*	-49.9
1969	8	1306.4*c*	1428.8*d*	90.7	9	1433.4*c*	1374.4*d*	226.8
1970	10	1351.7*e*	1270.1*d*	-158.8	10	1333.6*e*	1392.5*d*	18.1
1971	16	1297.3*e*	1369.9*f*	-54.4	15	1474.2*e*	1614.8*f*	140.6
1972	15	1369.9*g*	1428.8*f*	59.0	4	1374.4*g*	1592.1*f*	-22.7
1973	5	1134.0*g*	1315.4*h*	-235.9	12	1233.8*g*	1174.8*h*	-140.6
1974	2		811.9*h*	-503.5	4	1029.7*i*	997.9*h*	-176.9
1975	0		1320.0*i*		5	1515.0*i*	1574.0*j*	485.3
1976	4	1501.4*j*	1478.7*i*	158.8	8		1682.8*j*	167.8
1977	6	1705.5*j*	1959.5*k*	204.1	0		2091.1*k*	167.8
1978	2		1623.9*k*	-335.7	15		1764.5*k*	-326.6

[1]The same letters indicate means of repeated matings.

Table 6.15*b*. Distribution of observations, progeny means and yearly environmental changes of male yearling weight for the Hereford and Synthetic populations.

Year	HEREFORD			SYNTHETIC		
	No. of observations	Progeny means of repeated matings[1] (kg)	Environmental changes (kg)	No. of observations	Progeny means of repeated matings[1] (kg)	Environmental changes (kg)
1966		425.83*a*	0.00		460.47*a*	0.00
1967	7	433.68*a*	423.98*b*	7.85	15	493.41*a*	435.73*b*	32.94
1968	4	419.64*c*	476.71*b*	52.73	9	453.28*c*	451.74*b*	16.01
1969	8	426.74*c*	460.22*d*	7.10	9	493.41*c*	484.58*d*	40.13
1970	10	440.24*e*	424.02*d*	-36.20	10	478.00*e*	508.40*d*	23.82
1971	16	414.16*e*	429.15*f*	-32.08	15	490.71*e*	535.71*f*	12.71
1972	15	460.44*g*	458.70*f*	29.55	4	495.44*g*	529.94*f*	-5.77
1973	5	413.94*g*	429.79*h*	-46.50	12	465.20*g*	454.31*h*	-30.24
1974	2		309.06*h*	-120.73	4	414.06*i*	425.71*h*	-28.60
1975	0		440.21*i*		5	512.07*i*	536.44*j*	98.01
1976	4	486.75*j*	460.75*i*	20.53	8		535.39*j*	-1.05
1977	6	516.46*j*	565.22*k*	29.71	0		631.20*k*	0.00
1978	2		516.73*k*	-48.49	15		574.93*k*	-56.27

[1]The same letters indicate means of repeated matings.

Table 6.17. Distribution of observations, progeny means and yearly environmental changes of female 18-month weight for the Hereford and Synthetic populations.

Year	HEREFORD			SYNTHETIC		
	No. of observations	Progeny means of repeated matings[1] (kg)	Environmental changes (kg)	No. of observations	Progeny means of repeated matings[1] (kg)	Environmental changes (kg)
1966	371.20*a*		0.00	426.70*a*		0.00
1967	9 360.68*a*	386.51*b*	-10.52	14 417.86*a*	400.63*b*	-8.84
1968	5 318.78*c*	403.28*b*	16.77	3 408.12*c*	444.44*b*	43.81
1969	4 366.92*c*	398.32*d*	48.14	17 428.04*c*	397.80*d*	19.92
1970	10 376.41*e*	383.24*d*	-15.08	4 414.62*e*	445.75*d*	47.95
1971	8 369.45*e*	392.87*f*	-6.96	9 410.19*e*		-4.43
1972	2 385.67*g*	400.91*f*	8.04	0 398.50*f*		0.00
1973	9 370.57*g*	400.02*h*	-15.10	7 405.20*f*	397.90*g*	6.70
1974	13 332.49*i*	329.00*h*	-71.02	12 380.25*h*	375.19*g*	-22.71
1975	5 381.04*i*		48.54	11 415 62*h*	414.34*i*	35.37
1976	0 382.24*j*			22 423.08*j*	420.87*i*	6.53
1977	5 352.89*j*		-29.35	8 407.63*j*		-15.45

[1]The same letters indicate means of repeated matings.

Table 6.18. Yearly phenotypic means and standard errors, enviromental trends and genetic trends for female 18-month weight in the Hereford and Synthetic populations (kg).

Year	HEREFORD			SYNTHETIC		
	Pooled enviromental trend	Phenotypic mean±S.E.	Genetic response to selection	Phenotypic mean±S.E.		Genetic response to selection
1966	0.00	373.39±8.27	373.39	409.58±5.24		409.58
1967	-9.68	368.78±5.88	378.46	396.29±4.89		405.97
1968	20.61	375.80±7.88	355.19	400.77±6.89		380.16
1969	54.64	389.45±5.43	334.81	420.52±5.08		365.88
1970	71.07	382.96±5.84	311.89	415.88±4.90		344.81
1971	65.38	386.87±4.96	321.49	427.15±4.17		349.52
1972	73.42	389.89±6.39	316.47	415.14±4.72		341.72
1973	69.22	386.97±5.16	317.75	407.12±4.45		337.90
1974	22.35	320.63±5.73	298.28	368.10±3.94		345.75
1975	64.31	378.40±5.38	314.09	415.43±4.52		351.12
1976	57.78	388.42±9.96	330.64	422.11±3.97		364.33
1977	35.38	370.92±5.43	335.54	399.32±4.13		363.94
b=	4.00±2.22	-0.56±1.66	-4.56±1.65	-0.27±1.38		-4.23±1.63

Table 6.16a. Yearly phenotypic means and standard errors,enviromental trends and genetic trends for male postweaning ADG in the Hereford and Synthetic populations (gm/day).

	HEREFORD			SYNTHETIC		
Year	Pooled enviromental trend	Phenotypic mean±S.E.	Genetic response to selection		Phenotypic mean±S.E.	Genetic response to selection
1966	0.00	1213.36±40.10	1213.36	1260.53±32.66		1260.53
1967	154.22	1411.58±35.34	1257.36	1435.17±32.75		1280.95
1968	108.86	1296.37±34.43	1187.51	1247.38±30.80		1138.52
1969	267.62	1352.16±30.44	1084.54	1431.99±23.72		1164.37
1970	195.05	1306.35±28.12	1111.30	1364.41±28.21		1169.36
1971	240.40	1300.90±30.35	1060.50	1468.28±24.95		1227.87
1972	258.55	1406.59±32.30	1148.04	1455.58±23.63		1197.03
1973	68.04	1245.11±33.84	1177.07	1314.96±24.04		1246.92
1974	-272.16	1030.56±40.64	1302.72	1097.69±36.24		1369.85
1975	213.19	1213.36±38.06	1000.17	1515.45±24.49		1302.26
1976	267.62	1455.58±35.15	1187.96	1631.57±26.67		1363.95
1977	471.74	1695.07±32.61	1223.33	2008.05±24.04		1536.31
1978	136.08	1379.37±55.34	1243.29	1680.11±22.54		1544.03
b=	9.72±13.17	11.16±11.57	1.42±6.62		35.61±14.11	25.90±6.46

Table 6.16*b*. Yearly phenotypic means and standard errors,enviromental trends and genetic trends for male yearling weight in the Hereford and Synthetic populations (kg).

Year	HEREFORD			SYNTHETIC		
	Pooled enviromental trend	Phenotypic mean±S.E.	Genetic response to selection		Phenotypic mean±S.E.	Genetic response to selection
1966	0.00	409.14±9.98	409.14	444.14±8.40	444.26	
1967	20.39	437.48±9.09	417.09	471.01±8.42	450.62	
1968	54.76	447.91±9.02	393.15	452.83±7.92	398.70	
1969	78.38	435.71±7.82	357.33	488.25±6.09	409.87	
1970	66.00	436.55±7.23	370.55	487.50±7.25	421.50	
1971	46.62	416.98±7.81	370.36	495.44±6.41	448.82	
1972	70.40	453.74±8.30	383.34	502.26±6.08	431.86	
1973	32.03	428.64±8.70	396.61	484.24±6.17	452.21	
1974	-42.64	375.69±9.88	418.35	441.17±9.32	483.81	
1975	55.37	448.44±9.78	393.07	519.12±6.29	463.75	
1976	66.16	470.50±9.03	404.34	535.95±6.85	469.79	
1977	95.87	512.18±8.38	416.31	606.98±6.18	511.11	
1978	43.49	446.61±9.87	403.12	545.71±5.79	502.22	
b=	2.10±2.75	3.39±2.26	1.29±1.47		8.84±2.35	6.74±1.63

Phenotypic, environmental and genetic trends for the entire period studied were estimated by regressing yearly phenotypic least square means, yearly environmental trends and yearly responses to selection on years. Standard errors of the regression estimate were taken as the standard errors of the respective trends.

Results and Discussion

Preweaning traits

Estimates of phenotypic, environmental and genetic trends for birth weight, preweaning ADG and weaning weight from 1966-1978 are shown in Table 6.19. Phenotypic trends were positive for all traits with those for the Synthetic population being generally higher than those for the Hereford population.

Environmental trends were also positive over the period studied. Those for preweaning ADG were similar between breeds, suggesting no breed x environment interaction existed for preweaning growth. This type of interaction, however, may have existed in prenatal growth where the environmental trend was higher in Synthetics than Herefords.

Genetically, birth weight decreased over years with the Herefords decreasing 0.26 ± 0.12 kg/year and the Synthetics 0.27 ± 0.10 kg/year.

This is difficult to explain in view of the positive correlation between birth weight and other growth traits which have increased. Selection differentials for birth weight were found to be small but positive in both

populations. Most likely, environmental trends were overestimated for birth weight since genetic trends would be expected to be small but positive.

Positive genetic gains were seen in both population for preweaning growth traits. Hereford preweaning ADG increased by 3.25 ± 2.72 g/day/year as compared to 7.76 ± 3.25 g/day/year in the Synthetic. The respective values for weaning weight were 0.13 ± 0.60 kg/year and 0.93 ± 0.53 kg/year. These genetic gains were not greatly different from those predicted (2.65g/day/year for Herefords and 9.30 g/day/year for Synthetics) The estimated trends were considered fairly reliable.

Postweaning Traits

The phenotypic, environmental and genetic trends for postweaning ADG and yearling weight in males and 18-month weight in females are outlined in Table 6.20.

Phenotypic trends for postweaning growth in males were much higher in the Synthetics than the Herefords. Phenotypically the Synthetics' increase in yearling weight was 8.84 ± 2.35 kg/year as compared with 3.39 ± 2.26 kg/year in the Herefords. The respective values for postweaning ADG were 35.61 ± 14.11 g/day/year and 11.16 ± 11.57 g/day/year.

Genetic trend estimates for postweaning growth in the Synthetic population was likely an overestimation of the real trend for several reasons. Firstly, the accuracy of a pooled environmental trend relies on the assumption that no genetic x environmental interaction exists for the traits

Table 6.20. Estimates of phenotypic, environmental and genetic trends for postweaning ADG and yearling weight in males and 18-month weight in females.

Breed	Postweaning[1] ADG (g/day)	Yearling Weight[1] (kg)	18-month Weight (kg)[2]
	Phenotypic Trends		
Hereford	11.16 ± 11.57	3.39 ± 2.26	-0.56 ± 1.66
Synthetic	35.61 ± 14.11	8.84 ± 2.35	-0.27 ± 1.38
	Environmental Trends		
Pooled Breeds	9.72 ± 13.17	2.10 ± 2.75	3.99 ± 2.21
	Genetic Trends		
Hereford	1.42 ± 6.62	1.29 ± 1.47	-4.56 ± 1.65
Synthetic	25.90 ± 6.46	6.74 ± 1.63	-4.23 ± 1.63

[1] Includes males from 1966-1978.

[2] Includes females from 1966-1977.

under study (i.e., if some environmental factor changes by 1 unit, the response in both breeds will be equal). This assumption may not be true. If not, genetic trends in the Synthetics could possibly be overestimated while those in the Herefords, underestimated. Secondly, due to an irregularity in the raw data, postweaning means for 1977 calves contained an extreme upward bias. Unfortunately, in the Synthetic population, no sires producing progeny in 1976 were repeated in 1977. Thus the environmental change between

the 2 years was assumed to be that estimated from the Hereford population where the magnitude of the upward bias was not nearly as large. Thus the environmental change in 1977 was probably severly underestimated in the Synthetics and an excess of the high phenotypic values for postweaning traits in males was designated as genetic.

Phenotypic trends for 18-month weight in females were slightly negative; however, the pooled environmental trend was positive by 3.99 ± 2.21 kg/year. As a result a negative genetic trend of -4.56 ± 1.65 kg/year and -4.23 ± 1.63 kg/year was seen in Herefords and Synthetics respectively.

Again, these results are unexpected. With intensive selection for increased growth, 18-month weight in heifers would also be expected to increase genetically. The estimate of environmental trend was likely too high.

VII. Conclusions

Since problems existed in each of the three methods employed to estimate environmental and genetic trends for pre- and postweaning growth traits, precise estimations of trends during the period studied were difficult to determine. However, in general, several conclusions can be drawn concerning the genetic response in the purebred Hereford population as compared to that in the multibreed Synthetic population.

According to selection differentials realized in both populations, slightly more phenotypic variation for preweaning traits existed in the Synthetic population. The difference between populations was not as great as expected. In spite of the assumption that the purebred Herefords were genetically more homozygous than the Synthetics, there were no indications of loss of variability over time. This may be explained by the variance components estimated. Very little of the variation of the preweaning traits was of genetic nature. The genetic component was much higher in the Synthetics. This suggests that the preweaning traits in the Herefords was much more affected by environmental conditions than in the Synthetics. Thus, although the variation is present, the heritability of the trait is so low that only small genetic responses to selection can be expected. This was observed in preweaning ADG and weaning weight where the differences in genetic responses between the two populations were relatively greater than the differences in selection

differentials.

The situation for postweaning traits in males was somewhat different. The genetic component of total phenotypic variation was similar in both populations. Again, the selection differential realized in the Synthetics was higher than in the Herefords and thus, greater genetic increases could be expected in the Synthetic population, a result verified by all three methods of analysis.

Phenotypically, female 18-month weights had not changed greatly during the period studied. The control population method yielded a negative environmental trend over this time while the other two methods yielded positive environmental trends--thus negative genetic trends. Selection for reproduction in cows resulted in almost no selection differential realized for 18-month weight in females. However, logically, selection for increased growth in sires would also result in faster growing females. It is difficult to explain genetic decreases in this trait.

In general, genetic gains have been higher in the Synthetic population than in the Hereford. The greater genetic response resulted from larger selection differentials and a higher component of genetic variance in the Synthetic population. In conclusion, it seems that there exists greater opportunity for genetic progress by establishing a synthetic population of several breeds as a population base as opposed to selection from within an established breed.

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